MANAGEMENT STRATEGIES FOR CONSERVATION OF GENETIC DIVERSITY IN WOOD BISON *(Bison bison athabascae)*

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Executive Summary

Conservation of genetic diversity is essential to the long-term survival of any species, particularly in light of changing environmental conditions. Reduced genetic diversity may negatively impact the adaptive potential for a species. In addition, low genetic diversity leads to an increased risk of inbreeding effects, through the uncovering of deleterious recessive alleles. Consequently, management of genetic diversity is an important component of recovery strategies for threatened and endangered wildlife.

In Canada, the single greatest limiting factor affecting recovery of the threatened wood bison (*Bison bison athabascae)* is the presence of bovine tuberculosis *(Mycobacterium bovis)* and brucellosis *(Brucella abortus)* in and around Wood Buffalo National Park (WBNP). Despite the successful salvage of the founders for the Elk Island National Park (EINPW) and Mackenzie bison populations in the 1960s, and most recently the Hook Lake Wood Bison Recovery Project (HLWBRP), the majority of wood bison genetic diversity exists within the diseased populations of the Greater Wood Buffalo National Park Ecoregion. Genetic diversity in the Mackenzie and EINPW wood bison populations is substantially less than the wild populations from which they were salvaged, likely due to a combination of the founder effect and genetic drift. In addition, disease-free wood bison herds that have been established through national recovery efforts have been generally managed as small and genetically isolated populations, although some herds have received supplemental releases from the wood bison herd at EINPW. Thus, due to a series of founding events and population bottlenecks, genetic diversity is not well distributed among disease-free wood bison herds in Canada.

In this study, we used a simulation modeling approach to evaluate strategies for management of genetic diversity and maintenance of gene flow among disease-free wood bison herds. Within a metapopulation framework, we evaluated the relative effects of population size, number of populations, movement of animals between populations, and harvesting or culling regimens on genetic diversity. Based on current population genetic status and the influence of these factors on genetic diversity in simulated populations, we arrived at the following conclusions:

- Additional genetic salvage should be conducted from diseased bison in and around Wood Buffalo National Park to ensure that genetic diversity of wood bison is well represented and conserved in disease-free populations. Each salvage effort should be based on a large number of founding individuals, similar to the effort undertaken at the HLWBRP.
- The most genetically important disease-free populations should be the primary source for creating new disease-free populations.
- The HLWBRP represented one of the most genetically important populations because it was unrelated to EINPW and because it was established with a larger number of founders. However, genetic management of this population must continue to ensure diversity is not quickly lost due to its small size.[1]
- Herd size is the primary factor affecting the loss of diversity from the wood bison metapopulation through time. Management of individual wood bison herds

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[1] Unfortunately, a single case of bovine tuberculosis was confirmed in the HLWBRP in June 2005 (see Lutze-Wallace *et al.*, 2006). Subsequent disease testing and culling up until winter 2006 had confirmed that an additional five bison were infected with bovine tuberculosis. In March 2006, all remaining HLWBRP bison were destroyed.

above a minimum population size (i.e., census size $\geq$ 400 individuals) will minimize the loss of diversity.

- The movement of animals among all herds will significantly reduce the rate at which diversity is lost. However, assurance that populations remain large should take precedence over gene flow when populations are below carrying capacity.

Given the long-history of the northern diseased bison issue and the potential for infectious diseases to undermine conservation objectives, it will be equally important for wildlife managers to consider and balance genetic management objectives of wood bison, with disease and health management objectives. This will require objective and more quantitative assessments of risks and opportunities when considering translocation of bison for genetic management purposes.

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1.0 Introduction

The recovery of wood bison (*Bison bison athabascae*) in northern Canada will ultimately depend on conservation and management of genetic diversity among free-ranging populations of bison that are free from infection with bovine tuberculosis *(Mycobacterium bovis)* or brucellosis *(Brucella abortus)* (see Gates *et al.* 2001). In order for real progress in wood bison recovery to be made, wildlife managers will need to develop and implement recovery strategies that are centered on both disease eradication and genetic conservation objectives (see Connelly *et al.* 1990, Nishi *et al.* 2002b, Wilson *et al.*, 2005, Shury *et al.* 2006).

Here, our broad intent is to define the issues and develop strategies that are relevant to genetic conservation of wood bison. One of our primary motivators for conducting this work was to respond to the general need for a genetic management strategy as identified by the National Wood Bison Recovery Team (Gates *et al.* 2001), and the Governments of Yukon (Government of Yukon 1998) and British Columbia (Harper *et al.* 2000), which have formally recognized the importance of genetic management and augmentation within their respective wood bison recovery plans.

Another important motivator for this work was the Hook Lake Wood Bison Recovery Project (HLWBRP) (see Gates *et al.* 1998, Nishi *et al.* 2001, Nishi *et al.* 2002a, Wilson *et al.*, 2005). At the time we initiated this project, we were anticipating that captive-born bison from the HLWBRP might become available in the near future for national wood bison recovery efforts (see Nishi *et al.* 2002a and 2002b, APFRAN 2003, Nishi *et al.* 2004). As the HLWBRP wood bison represented a new source of genetic diversity that was salvaged from the Slave River Lowlands (Wilson 2001, Wilson *et al.*

2005), the recovery project represented a potentially valuable source for augmenting genetic diversity of existing conservation herds. However, prior to this project there was no well-developed rationale or genetic management strategy upon which specific recommendations for genetic augmentation of other wood bison conservation herds could be based.

Unfortunately, in June 2005, bovine tuberculosis was confirmed in a 3 year-old captive-born bull at the HLWBRP (Lutze-Wallace *et al.*, 2006). Subsequent disease testing and a preliminary epidemiological investigation in which 21 animals were euthanized indicated that at least 6 animals were infected with bovine tuberculosis (B. Elkin and J. Nishi, unpublished data). All remaining founder and captive-born animals were culled on site, or transported to abattoirs in Alberta in February and March 2006. However, for this report, we have included the HLWBRP according to our original research project design and analyses, because the results and implications are still relevant; indeed, the loss of the HLWBRP emphasizes the importance of genetic salvage for wood bison.

We suggest that there are two basic issues that are important for the genetic conservation of the threatened[2] wood bison in Canada. The first issue involves the management of genetic diversity within (Wilson and Zittlau 2004, Wilson *et al.*, 2005, Wilson *et al.*, in prep) and among disease-free[3] wood bison populations. The second is the relatively low proportion of genetic variability that is represented by existing disease-

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[2] Wood bison (*Bison bison athabascae*) are considered a threatened subspecies of North American Bison by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC); they are listed in Appendix II by the Convention on the International Trade In Endangered species (CITES).

[3] We use the term "disease-free" and "healthy" to describe bison herds that are free from infection with either bovine tuberculosis *(Mycobacterium bovis)* or brucellosis *(Brucella abortus)*.

free wood bison populations, compared to the diseased metapopulation in Wood Buffalo National Park (WBNP) (see Wilson and Strobeck 1999).

Disease-free wood bison herds established through national recovery efforts have been generally managed as relatively small (see Wilson and Zittlau 2004) and genetically isolated populations. Although some herds have received supplemental releases from the wood bison national recovery herd at Elk Island National Park (EINPW) (Gates *et al.*, 2001), it is likely that the founder effect and/or genetic drift has affected the levels of genetic diversity in some or all of these herds. Apart from the Mackenzie population, all other disease-free wood bison herds in Canada (Aishihik, Etthithun, Nordquist, Nahanni, Hay-Zama, Chitek Lake, Caribou Mountains-Lower Peace area, Waterhen and Syncrude) originate either directly or indirectly from the EINPW population. As such, we expect those populations to be less genetically variable than EINPW animals and hence, be among the least variable bison populations (Wilson and Strobeck 1999). With the exception of the Mackenzie and EINPW populations, there is a dearth of population genetic data from disease-free wood bison populations. Although those other populations are integral to national recovery efforts, the amount by which their genetic diversity has been reduced is unknown. Thus, it is important to evaluate whether current management of reintroduced, disease-free wood bison, which are maintained as genetically isolated populations, may have a negative impact on genetic diversity and population viability over the long term (see Halbert *et al.*, 2004, 2005). Correspondingly, there is a need to evaluate and develop strategies that would outline whether and how gene flow may be established among disease-free herds.

Despite salvage of healthy wood bison from WBNP in the 1960s to create the Mackenzie and EINPW populations (see Blyth 1995, Gates *et al.* 2001, Nishi *et al.* 2002b), the majority of genetic diversity still exists in the diseased wood bison populations of the Greater WBNP Ecoregion (Wilson and Strobeck 1999, Wilson *et al.* 2005). The genetic diversity in the Mackenzie and EINPW wood bison populations is substantially less than the wild populations from which they were salvaged, largely due to a combination of founder effect and genetic drift (Wilson and Strobeck 1999). Therefore, it is important to determine whether and how much additional genetic diversity from the diseased bison populations should be salvaged to ensure long-term survival and evolution of the subspecies in populations free from infection with bovine tuberculosis and brucellosis. Indeed, resolution of the larger northern diseased bison issue through depopulation of diseased bison and repopulation with healthy bison will likely be strongly linked to a decision on whether sufficient genetic salvage has been or will be achieved (see Shury *et al.* 2006)

In this report we take a broad genetic management perspective on conservation of wood bison in northern Canada, and outline strategies for:

1) establishing and maintaining gene flow between disease-free, reintroduced wood bison populations which historically existed as a panmictic population; and
2) conducting additional genetic salvage of wood bison from the diseased WBNP metapopulation.

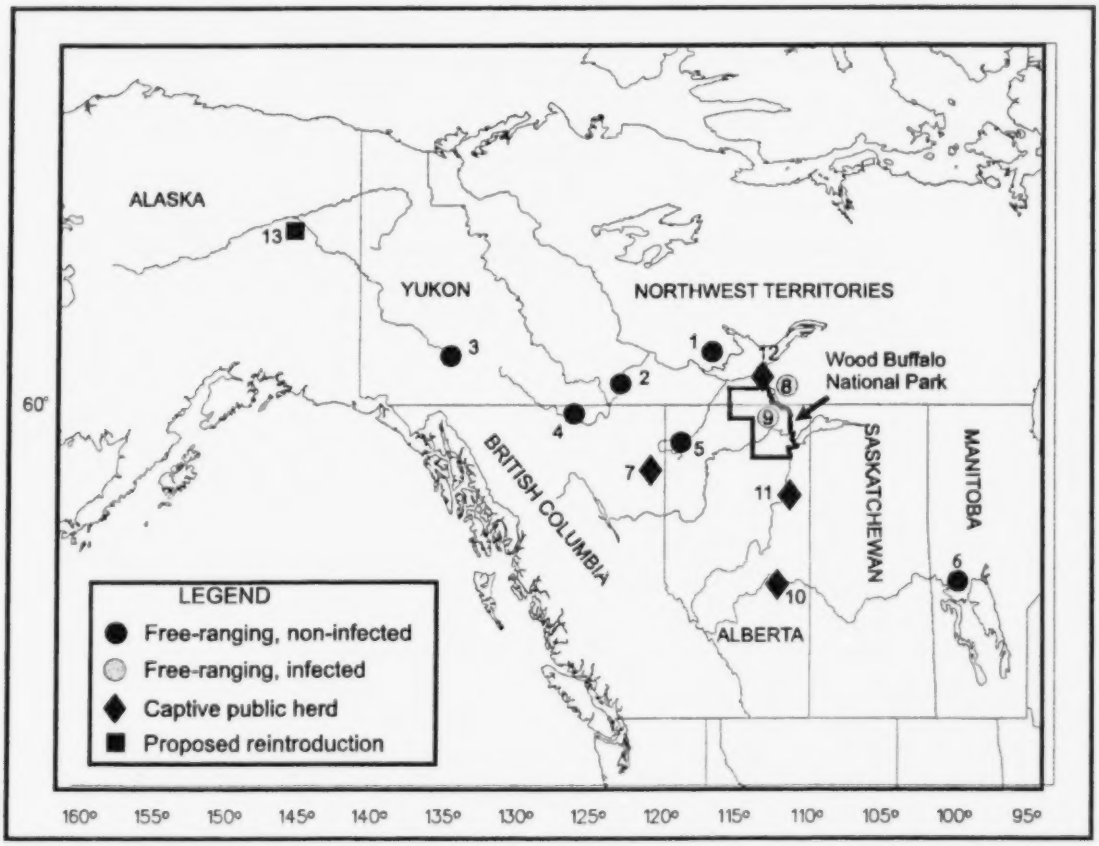
1.1 Background – wood bison

Wood bison declined from an estimated 100,000 to about 250 individuals by the beginning of the 20th century (Soper 1941 and see reviews by Gates *et al.* 1992, Stephenson *et al.* 2001, and Reynolds *et al.* 2003). By 1900, the geographic range of wood bison had shrunk accordingly, and their range was restricted to a part of the area currently known as Wood Buffalo National Park (WBNP). Following the enactment of a federal law in 1893 to protect the remaining wood bison and actual enforcement of the law by the Northwest Mounted Police starting in 1897, the number of bison increased over subsequent years (Soper 1941). By the time WBNP was created in 1922 to protect the remaining wood bison and their habitat (Figure 1) (Lothian 1976, 1979), the population was estimated at between 1500 and 2000 (Siebert and Soper, in Gates *et al.* 1992).

From 1925-1928, over 6,600 plains bison from Buffalo National Park in Wainwright, AB, were transported by rail and barge to WBNP (see Gates *et al.,* 1992, Fuller 2002, McEwan 1995). In addition to the resultant hybridization between the introduced plains bison and the indigenous wood bison, this translocation also introduced bovine tuberculosis (*Mycobacterium bovis*) and brucellosis (*Brucella abortus*) into the WBNP population (van Zyll de Jong 1986, Connelly *et al.,* 1990, Carbyn *et al.* 1993, Gates *et al.,* 2001, Fuller 2002, Joly and Messier 2004a).

The combined effect of disease (tuberculosis and brucellosis) and predation by wolves is hypothesized to be an important regulating factor in the population dynamics of WBNP bison (Messier 1989, Gates 1993, Gates *et al.* 1997, Joly and Messier 2004b, Joly and Messier 2005, but also see Carbyn *et al.,* 1993, Carbyn *et al.* 1998, Bradley

and Wilmshurst 2005). From a wildlife management perspective, the presence of diseased bison is considered to be the single greatest factor limiting the recovery of wood bison in northern Canada (Gates *et al.* 2001).



1 Mackenzie (MB)
2 Nahanni (NH)
3 Yukon (YK)
4 Nordquist (NQ)
5 Hay Zama (HZ)
6 Chitek Lake (CL)
7 Etthithun Lake (EL)
8 Slave River Lowlands (SRL)
9 Wood Buffalo National Park (WBNP)
10 Elk Island National Park (EINP)
11 Syncrude Canada Ltd. (SN)
12 Hook Lake Wood Bison Recovery Project (HLWBRP)
13 Yukon Flats (proposed)

Figure 1. Wood bison herds in Canada.

There have been three attempts to salvage disease-free wood bison from the WBNP area (see Blyth 1995, Gates *et al.*, 2001, and Nishi *et al.*, 2002b, Wilson *et al.*, 2005). In the 1960s herds were established from WBNP wood bison at the Mackenzie Bison Sanctuary (MB) and at EINPW. Areas adjacent to WBNP were the source for the HLWBRP (Figure 1, Table 1). However, due to an unrepresentative number of founders and small herd sizes, both of which can reduce genetic diversity, there are concerns about the levels of genetic diversity present within these herds and the rate at which it is being lost.

Table 1. Wood bison herds examined in this study.

Year Initiated	Herd	Capture Location	Number of Founders	Current Size	Carrying Capacity
-	WBNP	-	250 [a]	4500	5000
1963	MB	Needle Lake, WBNP	16	2000	2000
1965	EINPW	Needle Lake, WBNP	22	320	450
1980-1989	NH	EINPW	70	200	320
1986-1992	YK	EINPW [b]	142	530	530
1995	NQ	EINPW [b]	49	62	120
1996	HLWBRP	Hook Lake, Slave River Lowlands	57	120	125
	Total	-	-	**7727**	**8040**

[a] In this case, "founders" refers to the lowest number of animals estimated for this population in approximately 1900 (Soper 1941).

[b] Animals were also received from Moose Jaw Wild Animal Park and/or the Toronto Metro Park, both of which were derived from EINPW.

1.2 Background – genetic diversity

Conservation of genetic diversity is an essential aspect of the management of threatened and endangered species. Genetic diversity is vital for population viability. In

the short term, low levels of diversity can result in inbreeding depression, increasing the probability of population extirpation or reducing population fitness (Coulson *et al.* 1998, Saccheri *et al.* 1998, Puurtinen *et al.* 2004). The effects of inbreeding can accumulate over many generations, as the frequency of slightly deleterious alleles can gradually increase over time due to genetic drift (Lande 1994, Lande 1995, Lynch *et al.* 1995, Whitlock 2000). This is a particular concern in small populations, where natural selection can be inefficient for alleles that have only slight effects on fitness (Wright 1977).

Over the long-term, a paucity of genetic diversity will reduce the population's ability to adapt to changing environmental conditions and respond to natural selection pressures (Franklin 1980, Lacy 1987, Frankham *et al.* 1999). Furthermore, once unique genetic material is lost from a species it cannot be regained, even through the process of mutation. Genetic diversity can be lost through founder effects, population bottlenecks, genetic drift, and selection. The rate at which genetic diversity is lost will depend on the population's size and degree of isolation; small, isolated populations can lose genetic diversity within a few generations, whereas large, continuous populations may not lose significant amounts of diversity over thousands of years (e.g., Zittlau 2004). In small populations where genetic drift is most rapid, the fixation of common alleles will result in the reduction of genetic diversity.

If gene flow is inhibited, the diversity that is lost within a population each generation will not be replenished from other populations. Current management strategies treat wood bison herds as isolated units, with no gene flow occurring among them, suggesting they will be vulnerable to this phenomenon. The small size of many

wood bison populations makes them highly susceptible to the processes of genetic drift. However, as drift in subdivided populations can result in the fixation of different alleles in each population, overall metapopulation diversity can be higher in this scenario, as fixation of an allele guarantees that it will not be lost (Kimura and Crow 1963). Consequently, the proper management strategy to maximize diversity at the metapopulation level is not clear without further knowledge of the populations' demographic and genetic composition.

1.3 Measuring genetic diversity

Some commonly used measures of diversity are expected heterozygosity, probability of identity, allelic richness, the number of private alleles, and allelic proportion. Expected heterozygosity measures the proportion of a population that is expected to possess different alleles at a particular locus (Nei and Roychoudhury 1974). As such, it is a measure of the amount of variance in allele frequencies, and is maximized when these frequencies are equivalent across a locus. Unbiased probability of identity measures the probability that two individuals within a population have the same genotype (Paetkau *et al.* 1998). Probability of identity is also a measure of the evenness with which alleles are distributed at a locus. Allelic richness measures the mean number of alleles at a locus, weighted against the sample size of the population (El Mousadik and Petit 1996). Private alleles are alleles that occur only in a single population and, therefore, give a measure of the distinctiveness of each population (Kalinowski 2004). Finally, allelic proportion measures the proportion of alleles within a metapopulation that are found in each subpopulation. Populations that contain a large

amount of the diversity found within a metapopulation have a high allelic proportion value.

As a variety of genetic diversity measures exist, identification of the best measure is frequently debated. Many conservation geneticists feel that allelic richness is the most relevant measure of genetic diversity, because a large number of alleles will supply a source of variation upon which selection can act (e.g., Schoen and Brown 1993, Bataillon *et al.* 1996, Petit *et al.* 1998). Generally, selection of the most useful genetic diversity measures will be largely dependent on the problem being addressed. For example, information on expected heterozygosity, probability of identity, and allelic richness can be useful for determining which herds may be in danger of suffering inbreeding effects. Identification of private alleles and allelic proportion can be especially useful for identifying potential sources of highly variable individuals to add to any genetically depauperate herds.

1.4 Current population genetic status of wood bison herds

Lack of knowledge concerning population genetic diversity can complicate the implementation of genetic management efforts. Although previous studies have shown that the three populations of wood bison captured from the WBNP ecoregion are less variable than their founding population (Wilson and Strobeck 1999, Wilson *et al.* 2005), the diversity within any conservation herd founded from EINPW is currently unknown.

Attempts were made to collect samples from wood bison populations founded from EINPW for this study. However, where this was not possible, attempts were made to elucidate current levels of diversity through simulation techniques. Programs such as GENELOSS (England and Osler 2001) employ Monte Carlo sampling methods to simulate

the amount of diversity lost when populations are subjected to a bottleneck. As founding events essentially act as bottlenecks, this program is useful for estimating levels of diversity in populations for which DNA samples are unavailable. GENELOSS has proven valuable in estimating the magnitude of population bottlenecks in elk populations, based on current levels of diversity (Williams *et al.* 2004).

Determining the genetic importance of populations to metapopulation diversity is valuable for revealing where management efforts and resources can be best applied. If WBNP is to be depopulated and replaced with healthy wood bison, as recommended by a Federal Environmental Review Panel (Connelly *et al.* 1990, and see Shury *et al.* 2006), the genetic importance of this population to the wood bison subspecies must be examined to determine whether additional salvage attempts are required to sufficiently sample the genetic diversity in this region. Furthermore, potential sources of individuals from which to establish new conservation herds can be recognized if genetic importance is well understood. Due to differences in levels of diversity, all populations are not equally capable of responding to changes in environmental conditions. Therefore, an evaluation of the contribution of each population to the total metapopulation diversity, while simultaneously accounting for genetic divergence from other populations, was used to identify populations that have the highest evolutionary-response potential (Petit *et al.* 1998).

1.5 Estimating future diversity of wood bison

Due to forces such as genetic drift, differential reproductive success, and natural selection, an eventual decline in genetic diversity is unavoidable in natural populations when the process of mutation is not considered. Mutation occurs at an average annual

rate of 2.2×10^{-9} per base pair in mammalian genomes (Kumar and Subramanian 2002), and is only occasionally a significant force. In contrast, drift, differential reproduction, and selective forces can have substantial impacts on a population's ability to retain diversity over time. The effect of different management strategies on the rate at which genetic diversity is lost can be modeled using population viability analyses (PVA). This capacity, and its ability to estimate the probability of population extinction, has resulted in PVA becoming a critical tool for wildlife conservation and management.

PVA software packages can project the future viability of natural populations based on the effects of deterministic and stochastic processes. A number of PVA packages exist, which vary with respect to their goals, data requirements, and assumptions (for review, see Wilson *et al.* 2003). Previously, the PVA program VORTEX (Lacy *et al.* 2003) was determined to be the most suitable for estimating the future diversity of wood bison (Wilson *et al.* 2003). The VORTEX model closely resembles the life history of bison and can accommodate the large amount of information available for wood bison populations. The more information incorporated into a model, the greater the predictive ability it will have. VORTEX has been used to estimate the probability of population extinction in a bison population (Halbert *et al.* 2004), as well to evaluate strategies for minimizing loss of diversity in two Elk Island National Park bison populations (Wilson and Zittlau 2004).

VORTEX can model dispersal and translocation of animals among herds, allowing for the evaluation of management strategies at a metapopulation level. The definition of metapopulation used here follows Thomas and Gray (2002), who describe it as a group of populations among which actual or potential movements of animals can occur. As

most wood bison populations have been established and managed as isolated units, anthropogenic barriers, and not adaptive or genetic differences, primarily limit dispersal among populations. Consequently, the wood bison metapopulation is defined as all public herds of wood bison. While few reports exist of wood bison movements throughout their range prior to their decline in the 1800s, it is likely that all regions were joined by at least occasional animal movements (Roe 1970, Reynolds *et al.* 2003). Therefore, the designation of a single wood bison metapopulation in Canada is warranted.

Proper conservation of the threatened wood bison requires an evaluation of the effectiveness of various strategies for genetic management. We used VORTEX to outline potential management strategies for maximizing the retention of genetic diversity over the next 500 years. We also used VORTEX to estimate the genetic effects of establishing gene flow among wood bison herds.

1.6 Objectives

By integrating analyses of genetic diversity and population viability, we:

1. determined the levels of genetic diversity in all populations, either from previous studies, the collection and analysis of DNA samples, or the use of simulation studies.
2. calculated the genetic importance of wood bison populations to determine how diversity is distributed throughout the metapopulation, and established the importance of the diseased WBNP animals to the total metapopulation diversity.

3. modeled the rate of change, over the next 500 years, in levels of genetic diversity for the wood bison populations in WBNP, EINPW, MB, HLWBRP, Yukon (YK), Nahanni (NH), and Nordquist (NQ).
4. modeled the rate of change, over the next 500 years, in levels of genetic diversity for the entire wood bison metapopulation.
5. evaluated various management options with respect to their effect on the genetic diversity of the metapopulation and on the projected degree of relatedness among subpopulations. These management scenarios are described further in Section 2.4, *Management scenarios modeled*.

2 Methods

2.1 Genotype analyses

To examine the genetic diversity in various salvaged herds of wood bison, tissue samples from the Yukon population were obtained and compared with previously published data from the EINPW, MB, WBNP, and HLWBRP populations (Wilson and Strobeck 1999). Where possible, the EINPW dataset was expanded from 36 to 218 individuals, isolated from a previous study on parentage, which included approximately 95% of the adults in the 1998 population (Wilson *et al.* 2002).

DNA was isolated from YK wood bison tissue samples using a QIAamp® Tissue Extraction Kit (QIAGEN Inc., Mississauga, ON). The DNA was analyzed at the same 11 microsatellite loci used in previous bison studies (Wilson and Strobeck 1999, Wilson *et al.* 2005) to ensure that the results were directly comparable. The expanded EINPW dataset was available for five loci: BM2830, BMC1222, and BM1225 (Bishop *et al.* 1994), BOVFSH (Moore *et al.* 1992), and RT29 (Wilson and Strobeck 1999). This expanded dataset was used in all population-level analyses described below, but was not used for the individual-level analyses due to the large number of unknown genotypes that would result. Primers were fluorescently labeled with FAM, HEX, or TET dye groups, and PCR conditions were as in Wilson and Strobeck (1999). PCR products were visualized on an ABI 377 DNA Sequencer.

2.2 Genetic diversity

Loci examined in the YK population were tested for heterozygote deficiencies using a Markov chain algorithm in GENEPOP 3.4 (Raymond and Rouset 1995). Linkage

disequilibrium between loci was also examined using GENEPOP 3.4. As BM4513 was monomorphic, this locus was not included in the pairwise tests for linkage disequilibrium. Error rates for both tests were adjusted to 0.05 using a Dunn-Sidák correction (Sokal and Rohlf 1995). Genetic variation was measured as allelic richness, average unbiased expected heterozygosity (Nei and Roychoudhury 1974), overall unbiased probability of identity (Paetkau *et al.* 1998), number of private alleles, and allelic proportion. These values were compared with those derived for the previously examined wood bison populations of WBNP, EINPW, and MB.

A G-test and an assignment test were used to determine the distinctiveness of the YK population from other wood bison populations. The G-test was performed using pairwise comparisons between YK and all other wood bison populations, summed over all loci (Sokal and Rohlf 1995). The assignment test (Paetkau *et al.* 1995; available at http://www.biology.ualberta.ca/jbrzusto/Doh.php) was performed among all genotyped wood and plains bison populations as described in Wilson *et al.* (2005).

Genetic distance measures can reveal the level of relatedness between populations. Nei's standard genetic distance, D_S (Nei 1973), was calculated among all wood bison populations using a program available at http://www.biology.ualberta.ca/jbrzusto/GeneDist.php. A neighbour-joining unrooted tree (Saitou and Nei 1987) created with PHYLIP 3.61 (Felsenstein 1995) was used to visualize genetic distances.

For any population where DNA samples were unavailable, Monte Carlo sampling was performed using the program GENELOSS (England and Osler 2001) to estimate the effects of the bottleneck or founding event on genetic diversity. First, however,

GENELOSS was used to estimate diversity in the YK population. These results were then compared to results of DNA analyses, in order to test the ability of GENELOSS to accurately estimate genetic diversity in bison populations.

GENELOSS requires information on initial allele frequencies at all loci of interest within a population, the number of effective breeding pairs during the bottleneck, and the generational length of the bottleneck. As the YK herd was primarily founded from the wood bison at EINPW, allele frequencies from the latter population could be used to approximate initial values prior to the bottleneck. The number of effective breeding pairs in the YK population was estimated knowing that the effective size of bison populations is approximately 1/3 that of the actual size (Wilson and Zittlau 2004). From 1986 to 1992, 142 wood bison from EINPW were obtained for the YK herd (Gates *et al.* 2001, Table 1). The effective number of founders for this population is, therefore, approximately 47 and the number of effective breeding pairs, rounded to the nearest whole number, is 24. As the YK population received an influx of founders over a six-year period, estimating the number of generations since its inception is not straightforward. However, if we assume a generation time of five years based on the minimum age of male reproduction observed in wood bison at EINPW (Wilson *et al.* 2002), between two and four generations have passed since the establishment of the YK population. Consequently, simulations were performed with bottleneck durations of between two and five generations. Simulated values for allelic diversity and heterozygosity were considered significantly different from those observed in YK if the latter values were not included within the 95% confidence interval. Three thousand iterations were performed for each scenario.

The NH and NQ populations were also founded from EINPW wood bison (Table 1), so allele frequencies from EINPW could be used as initial allele frequencies for these population simulations as well. The NQ population was founded from 49 individuals in 1995, but only 36 individuals were counted in 1996 (Gates *et al.* 2001). Therefore, either six or eight breeding pairs founded this population, and two or three generations have passed since its inception. The history of the NH population is substantially more complicated than that for either the YK or NQ populations. After being founded in 1980, individuals were added to NH in 1989 (from Moose Jaw Wild Animal Park) and 1997 (from EINPW; Gates *et al.* 2001). The NH population has also undergone numerous fluctuations in size. Consequently, estimating the number of founding breeding pairs requires several assumptions for which little information is available. As such, any estimates of diversity for NH based on our current knowledge of its number of founders are likely unreliable and, therefore, this population was not included in the GENELOSS analyses.

The contribution of each population to the genetic diversity of the metapopulation was measured using the program CONTRIB (Petit *et al.* 1998). While traditional measures of genetic diversity, such as those mentioned above, can assess the levels of genetic variation within a number of populations, they do not reveal the relative conservation value of the diversity present within populations. Two measures of genetic diversity can be directly compared across populations: unbiased expected heterozygosity, and allelic richness. As the number of alleles sampled from a population increases with sample size, variance in sample size must be allowed for if allelic richness is to be used for determining genetic importance. This was done using

rarefaction, a technique for sampling alleles in each population to allow for sample size differences (Hurlbert 1971). Rarefaction was performed with 25 individuals, as this value must be lower than the smallest population sample size (Table 3). The contribution to overall diversity was also partitioned into two components: the proportion resulting from the diversity of the population of interest, and the proportion due to the divergence of the population from all others (Petit *et al.* 1998). As locus BM4513 was monomorphic in the wood bison populations examined, it was not included in this analysis. The genetic importance of each population was also calculated after the removal of WBNP from the data set to determine the relative importance of the disease-free wood bison populations to metapopulation genetic diversity.

2.3 Simulating loss of diversity over time

VORTEX 9.40 (Lacy *et al.* 2003) was used to model the change in genetic diversity over time for individual herds and the wood bison metapopulation. Locations of the seven herds examined are indicated in Figure 1. VORTEX simulates the change in genetic diversity under the effects of various deterministic and stochastic processes. Although VORTEX has high data requirements, there is considerable information regarding bison available from historical records, annual census data, and published literature. The availability of demographic data varies greatly among the herds, and input variables were determined according to data quality and abundance (Table 2). For populations with little or low-quality data, input variables were estimated from the literature or from the EINPW herd, for which a vast amount of detailed demographic data is available (Table 2). The carrying capacity for each herd that was not heavily

managed was estimated from the range size and habitat productivity (Table 2). All estimates were based on predictions made in 2003.

2.4 Management scenarios modeled

We projected the change in genetic diversity resulting from four scenarios:

1. Present demographic distributions were used to project the future diversity according to current harvesting regimens and carrying capacities. Scenarios were modeled from the date of herd establishment until the year 2500, with founding animals taken from the source populations indicated in Table 1.
2. Individual herds were modeled independently to project the loss of genetic diversity over time when all alleles in the founding individuals are considered to be unique. This would demonstrate the extent to which genetic diversity has been lost from these herds due to founding effects during their establishment. These results can be contrasted to Scenario 1, in which each population's alleles are sampled from their source population of either EINPW or WBNP.
3. The value of maintaining multiple herds within the metapopulation was examined by modeling the existence of different numbers and combinations of herds. Results were then compared to the existing scenario with all seven herds belonging to the metapopulation. This projection also indicates each herd's contribution to metapopulation diversity. The modeled combinations are as follows:
    a) The metapopulation was modeled according to demographic distributions if only WBNP had been established.

b) The metapopulation was modeled according to demographic distributions if only WBNP, EINPW and MB had been established.

c) The metapopulation was modeled according to demographic distributions if all but the HLWBRP herd had been established.

d) The removal of WBNP was modeled to project the impact that a depopulation of the WBNP herd would have on the genetic diversity of the metapopulation. The entire age- and sex-classes were harvested in the year 2020, 120 years since the herd's establishment.

4. Metapopulation management options were evaluated by modeling the influence of various harvesting and translocation strategies on the change in genetic diversity over the next 500 years.

a) Gene flow among all herds was modeled by annually moving an equal number of animals from each herd, with the exception of WBNP, into each of the other herds. No animals were translocated from WBNP due to the risk of spreading disease. Also, no animals were moved into HLWBRP, because the carrying capacity of HLWBRP was small and the health status of the HLWBRP was still uncertain[4]. Simulated movements of animals ranged from five female and five male calves/year, to ten female and ten male calves/year. Only calves were used in translocations, and all calves were assumed to survive the translocation process.

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[4] We completed this project under the assertion that the HLWBRP was disease-free and conducted these analyses prior to the confirmation of tuberculosis in the HLWBRP in June 2005 (see Introduction).

b) Movements of animals from HLWBRP were modeled to project the effect of increased gene flow from this herd on the overall diversity of the metapopulation. A total of 20 male and female calves from HLWBRP were moved annually into the MB, EINPW, NH, YK, and NQ herds. Only calves were used in translocations, and all calves were assumed to survive the translocation process.

c) As MB has the largest population size of the disease-free herds and is thus most able to contribute animals to other populations without suffering size reductions, the genetic effects of moving animals from this herd were also examined. A total of 20 male and female calves from MB were moved annually into the EINPW, NH, YK, and NQ herds. Only calves were used in translocations, and all calves were assumed to survive the translocation process.

d) To examine the genetic contribution of the NH, YK, and NQ herds, gene flow among only these herds was examined. In addition, gene flow from all herds, except WBNP, into NH, YK, and NQ was modeled, as well as movements of bison from only EINPW, MB, and HLWBRP into only NH, YK, and NQ. A total of 20 male and female calves were moved annually, only calves were used in translocations, and all calves were assumed to survive the translocation process.

e) The genetic implications of additional salvage attempts were modeled by establishing one to three new herds of wood bison, consisting of the same demographic structure as the original HLWBRP herd, either in 2016 (20

years after HLWBRP establishment), or at 10-year intervals in 2016, 2026, and 2036. No gene flow occurred in these scenarios.

Table 2. Source of data for population viability analyses (PVA) of Canadian wood bison herds.

	Source of Data for Each Herd						
Data	**WBNP**	**MB**	**EINPW**	**NH**	**YK**	**NQ**	**HLWBRP**
Inbreeding rate	Ralls *et al.* 1988	Ralls *et al.* 1988	Ralls *et al.* 1988	Ralls *et al.* 1988	Ralls *et al.* 1988	Ralls *et al.* 1988	Ralls *et al.* 1988
Calf mortality rate	Reynolds *et al.* 2003	Gates and Larter 1990	Herd-specific data	Reynolds *et al.* 2003	Reynolds *et al.* 2003	Reynolds *et al.* 2003	Herd-specific data
Adult & juvenile mortality rate	Fuller 1966	Gates and Larter 1990	Herd-specific data	Fuller 1966	Fuller 1966	Fuller 1966	Herd-specific data
Female reproduction	Fuller 1966	Gates and Larter 1990	Herd-specific data	Fuller 1966, Gates and Larter 1990	Fuller 1966, Gates and Larter 1990	Fuller 1966, Gates and Larter 1990	Herd-specific data
Male reproduction	EINPW [a]	EINPW [a]	Herd-specific data	EINPW [a]	EINPW [a]	EINPW [a]	EINPW [a]
Sex & age distribution	EINPW [a]	Herd-specific data	Herd-specific data	Herd-specific data	Herd-specific data	Herd-specific data	Herd-specific data

[a] Estimated from EINPW data, provided by W. Olson, pers. com. 2003.

3.0 Results

3.1 Existing genetic diversity

3.1.1 Measured genetic diversity

Four of the loci (Eth121, RT24, BOVFSH, and RT29) were found to have a deficiency of heterozygotes in the YK population ($P > 0.05$). Only Eth121 was deficient of heterozygotes when the Dunn- Sidák experiment-wise error rate was used ($P > 0.05$). Of the 45 pairwise tests for linkage disequilibrium, four were found to be significant ($P > 0.05$). However, none of these were significant when the Dunn- Sidák experiment-wise error rate was used.

The genetic diversity present in YK and other wood bison populations is shown in Table 3. The WBNP population was the most variable according to all measures. MB had the lowest heterozygosity, while YK was the least variable based on probability of identity and allelic richness measures (without correction for sample size). YK had lower levels of diversity than EINPW, its founding population, based on all measures. There were a total of eight private alleles, seven of which occurred in the WBNP population. A total of 74 alleles were observed in all populations. Of these, a high of 72 (allelic proportion = 0.973) were observed in WBNP and a low of 40 (allelic proportion = 0.541) were observed in YK. When WBNP was excluded from the analysis, the total number of alleles observed decreased to 66, or 0.892 of the total when WBNP is included. The number of private alleles observed in HLWBRP increased to 13 when WBNP was excluded from the analysis, and the allelic proportion increased to 0.924, the highest of all populations sampled (Table 4).

Table 3. Existing genetic diversity in wood bison herds.

Herd	Sample Size	He	1/pI	Allelic Richness	# Private Alleles	Allelic Proportion
WBNP	81	0.552 [b]	5.7×10^{7} [b]	6.55 [b]	7	0.973
MB	28	0.441 [b]	7.6×10^{5} [b]	4.27 [b]	0	0.635
EINPW	36/218 [a]	0.517	1.4×10^{6}	4.09	0	0.608
YK	26	0.483	7.1×10^{5}	3.64	0	0.541
HLWBRP	57	0.508 [b]	5.8×10^{6} [b]	5.55 [b]	1	0.824
Total		**0.515** [c]				

[a] Combined estimate from 36 individuals used in Wilson and Strobeck (1999) and, where possible, all adult individuals in the 1998 population.

[b] From Wilson and Strobeck 1999.

[c] Calculated as mean heterozygosity for all populations where this value is known, weighted by total population sizes.

Table 4. Private alleles and allelic proportion when WBNP is excluded from the analysis.

Herd	Private Alleles	Allelic Proportion
MB	3	0.712
EINPW	0	0.682
YK	0	0.606
HLWBRP	13	0.924

3.1.2 Genetic distinctness of populations

Pairwise G-test comparisons revealed that YK was significantly different from all other populations ($P < 0.001$). Despite changes in allelic richness from those reported by Wilson and Strobeck (1999), the extended EINPW dataset was not significantly different from the previous EINPW dataset at the $P > 0.1$ level (Table 3).

Assignment test results are presented in Table 5. Most wood bison (61%) were assigned to the correct population and only four animals were incorrectly assigned across subspecies. All four of these bison were from WBNP. While 73% of the YK

individuals were correctly assigned, a fairly large proportion of them (19%) were misassigned to EINPW.

Table 5. Assignment test results. Numbers in parentheses are the proportion of assigned individuals. Individuals assigned to their own population are in bold. The "plains bison" column includes individuals assigned to any plains bison population.

Source Populations	Sink Populations					
	WBNP	MB	EINPW	YK	HLWBRP	Plains bison
WBNP	**39 (0.48)**	6 (0.07)	4 (0.05)	3 (0.04)	25 (0.31)	4 (0.05)
MB	3 (0.11)	**21 (0.75)**	0	0	4 (0.14)	0
EINPW	2 (0.06)	2 (0.06)	**28 (0.78)**	3 (0.08)	1 (0.03)	0
YK	0	1 (0.04)	5 (0.19)	**19 (0.73)**	1 (0.04)	0
HLWBRP	16 (0.28)	6 (0.11)	0	3 (0.05)	**32 (0.56)**	0

Genetic distances between all wood bison population pairs are in Table 6. Distances were generally smallest between WBNP and the other populations, and largest between MB and the other populations. Distances between HLWBRP and the other populations also tended to be small. The smallest observed distance was between WBNP and the HLWBRP (0.018), and largest was between YK and MB (0.166). The distance between YK and EINPW, at 0.041, was the second smallest observed.

The unrooted neighbour-joining tree depicting the genetic distances among all populations is illustrated in Figure 2. The YK-EINPW nodes are proximately located on this tree, as are the HLWBRP and WBNP nodes. The MB node is farthest from the other external nodes.

Table 6. D_S distances between wood bison populations.

Herd	WBNP	MB	EINPW	YK	HLWBRP
WBNP	0	0.074	0.051	0.063	0.018
MB		0	0.141	0.166	0.058
EINPW			0	0.041	0.074
HLWBRP				0.068	0

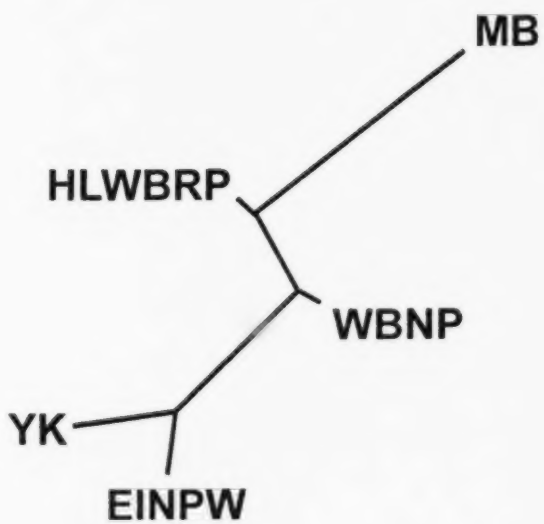

Figure 2. Neighbour-joining unrooted D_S tree of wood bison populations.

3.1.3 Estimated genetic diversity

Numbers of alleles and expected heterozygosity that were observed in the YK population and estimated from GENELOSS simulations for the pre-founding event and five subsequent generations are shown in Tables 7 and 8. Note that the GENELOSS

heterozygosity measure is not unbiased, as were the heterozygosity measures discussed above, and is thus not directly comparable to those values. Locus BM4513 was not included in the simulations, as it only contains a single allele in these populations. Overall, the number of alleles observed in YK was greater than that predicted under any simulated scenario. However, the observed number of alleles fell outside of the 95% C.I. at only two loci. The simulations for locus BM143 consistently had fewer alleles than observed in the YK population. In fact, more alleles were observed in YK at this locus than in EINPW, its founding population. The observed number of alleles at YK locus RT24 was less than the 95% C.I. for simulations of two and three generations, but not for greater numbers of generations.

The overall heterozygosity observed in YK was less than that found in each of the simulations. However, the heterozygosity values fell beyond the 95% C.I. at only two loci. Similar to the results for numbers of alleles, observed heterozygosity at locus BM143 was greater than the 95% C.I. in all simulations, while heterozygosity at RT24 was below the 95% C.I. in all simulations.

Table 7. Numbers of alleles sampled in the YK wood bison population and estimated from GENELOSS simulations for the pre-founding event and five subsequent generations. The number of breeding pairs was set at 24 for all simulations. Values in parentheses are standard deviations. Values in bold are not contained within the 95% C.I., with the observed value being either too high (superscript 'H') or too low (superscript 'L').

Locus	Initial (pre-founding event)	Sampled	Simulated Mean for Number of Generations			
			2	3	4	5
BM2830	6	5	4.31 (0.55)	4.19 (0.54)	4.07 (0.55)	3.96 (0.57)
BMC1222	3	3	3.00 (0.03)	3.00 (0.05)	2.99 (0.10)	2.98 (0.14)
BM1225	5	5	4.88 (0.34)	4.73 (0.47)	4.59 (0.57)	4.45 (0.63)
BOVFSH	9	6	6.83 (0.72)	6.52 (0.81)	6.21 (0.86)	5.97 (0.91)
RT29	7	6	6.03 (0.68)	5.81 (0.69)	5.63 (0.72)	5.50 (0.75)
BM143	3	4	**2.56^{H} (0.50)**	**2.47^{H} (0.50)**	**2.39^{H} (0.49)**	**2.35^{H} (0.48)**
Eth121	3	3	3.00 (0.04)	2.99 (0.09)	2.98 (0.12)	2.97 (0.16)
RT24	3	2	**2.98^{L} (0.13)**	**2.97^{L} (0.18)**	2.93 (0.25)	2.89 (0.31)
RT27	2	2	2.00 (0)	2.00 (0)	2.00 (0)	2.00 (0)
RT9	3	3	2.97 (0.17)	2.93 (0.26)	2.87 (0.33)	2.82 (0.38)
Total	4.4 (2.27)	3.9 (1.52)	3.86 (1.60)	3.76 (1.50)	3.67 (1.41)	3.59 (1.34)

Table 8. Heterozygosity sampled in the YK wood bison population and estimated from GENELOSS simulations for the pre-founding event and five subsequent generations. The number of breeding pairs was set at 24 for all simulations. Values in parentheses are standard deviations. Values in bold are not contained within the 95% C.I., with the observed value being either too high (supercript 'H') or too low (superscript 'L').

Locus	Initial (pre-founding event)	Sampled	Simulated Mean for Number of Generations			
			2	3	4	5
BM2830	0.593	0.556	0.580 (0.052)	0.576 (0.064)	0.570 (0.074)	0.562 (0.083)
BMC1222	0.587	0.551	0.576 (0.038)	0.572 (0.047)	0.565 (0.054)	0.558 (0.063)
BM1225	0.524	0.417	0.512 (0.075)	0.505 (0.088)	0.499 (0.104)	0.495 (0.111)
BOVFSH	0.682	0.697	0.668 (0.057)	0.662 (0.069)	0.655 (0.081)	0.646 (0.090)
RT29	0.752	0.754	0.736 (0.035)	0.727 (0.043)	0.721 (0.051)	0.715 (0.055)
BM143	0.513	0.654	**0.502^{H} (0.021)**	**0.497^{H} (0.030)**	**0.492^{H} (0.036)**	**0.487^{H} (0.041)**
Eth121	0.589	0.532	0.578 (0.034)	0.570 (0.045)	0.565 (0.051)	0.559 (0.056)
RT24	0.511	0.234	**0.501^{L} (0.053)**	**0.496^{L} (0.064)**	**0.491^{L} (0.073)**	**0.486^{L} (0.079)**
RT27	0.444	0.426	0.434 (0.046)	0.530 (0.057)	0.425 (0.065)	0.422 (0.072)
RT9	0.452	0.391	0.444 (0.065)	0.440 (0.076)	0.432 (0.090)	0.428 (0.099)
Total	0.565 (0.097)	0.521 (0.158)	0.553 (0.095)	0.547 (0.094)	0.542 (0.094)	0.537 (0.093)

As the ability of GENELOSS to estimate diversity in bison populations was confirmed by the similarities between observed and simulated values for YK, simulations were also performed to predict the diversity present in the NQ population. Simulated numbers of alleles for this population are shown in Table 9. There is little difference in the number of alleles between the scenario simulated for 2 generations with 6 breeding pairs and the scenario simulated for 3 generations with 8 breeding pairs. All simulated values are lower than those for the YK population.

Simulated levels of heterozygosity in NQ are shown in Table 10. The differences in diversity between the scenario with 6 breeding pairs over 2 generations and 8 breeding pairs over 3 generations are amplified when heterozygosity is examined. As with the number of alleles, all simulated heterozygosity values for NQ are lower than those simulated for the YK population.

Table 9. Pre-founding event number of alleles and simulated number of alleles for the NQ wood bison population. Values in parentheses are standard deviations.

Locus	Initial (pre-founding event)	Number of Generations			
		2	2	3	3
		Number of Reproductive Pairs			
		8	6	8	6
BM2830	6	3.69 (0.65)	3.44 (0.71)	3.44 (0.70)	3.20 (0.73)
BMC1222	3	2.93 (0.25)	2.86 (0.35)	2.86 (0.35)	2.77 (0.42)
BM1225	5	4.04 (0.76)	3.75 (0.84)	3.71 (0.83)	3.35 (0.88)
BOVFSH	9	5.36 (0.96)	4.87 (1.00)	4.87 (1.00)	4.34 (1.00)
RT29	7	5.12 (0.74)	4.80 (0.79)	4.80 (0.81)	4.47 (0.83)
BM143	3	2.26 (0.44)	2.20 (0.40)	2.19 (0.39)	2.14 (0.35)
Eth121	3	2.91 (0.29)	2.84 (0.36)	2.83 (0.38)	2.74 (0.44)
RT24	3	2.78 (0.41)	2.66 (0.48)	2.67 (0.47)	2.56 (0.51)
RT27	2	2.00 (0)	2.00 (0.03)	2.00 (0.03)	1.99 (0.10)
RT9	3	2.70 (0.46)	2.56 (0.51)	2.58 (0.50)	2.47 (0.53)
Total	4.4 (2.27)	3.38 (1.15)	3.20 (1.01)	3.20 (1.00)	3.00 (0.85)

Table 10. Pre-founding event expected heterozygosity and simulated heterozygosity for the NQ wood bison population. Values in parentheses are standard deviations.

Locus	Initial (pre-founding event)	Number of Generations			
		2	2	3	3
		Number of Reproductive Pairs			
		8	6	8	6
BM2830	0.593	0.557 (0.090)	0.542 (0.107)	0.539 (0.111)	0.522 (0.124)
BMC1222	0.587	0.553 (0.071)	0.540 (0.083)	0.536 (0.087)	0.523 (0.101)
BM1225	0.524	0.490 (0.124)	0.484 (0.141)	0.473 (0.145)	0.455 (0.164)
BOVFSH	0.682	0.641 (0.097)	0.628 (0.111)	0.622 (0.117)	0.606 (0.125)
RT29	0.752	0.703 (0.063)	0.692 (0.072)	0.683 (0.079)	0.666 (0.090)
BM143	0.513	0.483 (0.049)	0.472 (0.061)	0.467 (0.066)	0.450 (0.082)
Eth121	0.589	0.554 (0.062)	0.541 (0.078)	0.536 (0.080)	0.519 (0.098)
RT24	0.511	0.481 (0.094)	0.469 (0.105)	0.464 (0.109)	0.452 (0.124)
RT27	0.444	0.417 (0.081)	0.407 (0.092)	0.405 (0.097)	0.390 (0.115)
RT9	0.452	0.426 (0.110)	0.414 (0.121)	0.412 (0.127)	0.405 (0.140)
Total	0.565 (0.097)	0.530 (0.091)	0.519 (0.090)	0.515 (0.088)	0.499 (0.087)

3.1.4 Estimated genetic contribution

The contribution of each wood bison population to overall diversity, based on unbiased expected heterozygosity, is presented in Table 11 and Figure 3. Values of heterozygosity shown in Table 11 differ from those reported in Table 3 due to the exclusion of the monomorphic locus BM4513 in the analysis of genetic importance. If the mean heterozygosity is taken from 11 loci (when heterozygosities of monomorphic loci are 0), values become identical to those in Table 3. Populations with a below-average contribution to metapopulation diversity have negative genetic importance

values. WBNP has the highest genetic importance and the largest contribution to the total diversity of wood bison. This is even more evident when only the contribution due to the diversity within each population is considered. WBNP's contribution to genetic diversity is below average when considering population divergence. HLWBRP, MB and YK have negative total genetic importance values, but when the contribution to divergence is not considered, only MB and YK make negative contributions to diversity.

Table 11. Genetic contribution of each wood bison population to the total diversity, measured as unbiased expected heterozygosity, He. C_T represents the total contribution of each population to wood bison diversity, C_S represents the amount of this contribution due to each population's diversity, and C_D represents the amount of this contribution due to each population's divergence.

Herd	He	C_T	C_S	C_D
WBNP	0.586	0.010300	0.024200	-0.013800
MB	0.485	-0.005590	-0.027600	0.022090
EINPW	0.569	0.008300	0.008070	0.000168
YK	0.532	-0.003980	-0.007920	0.004000
HLWBRP	0.559	-0.009130	0.003720	-0.012400

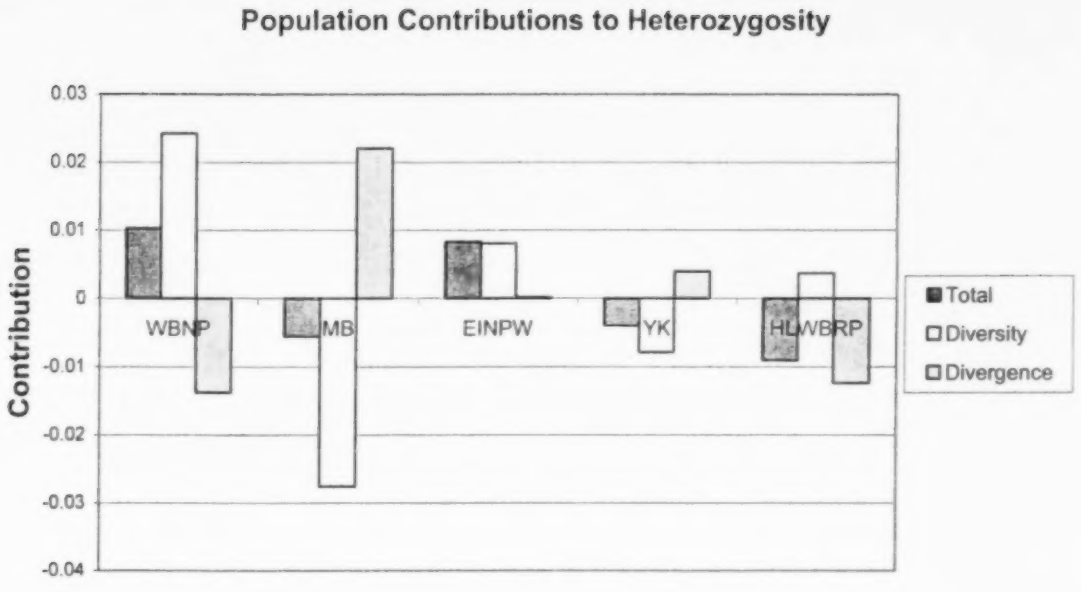

Figure 3. Contributions of each population to total wood bison diversity, measured as unbiased expected heterozygosity.

Allelic richness with rarefaction and each population's contribution to total diversity based on this measure are shown in Table 12 and Figure 4. Calculating allelic richness with rarefaction only slightly changes the order of population ranks compared to ranks determined without weighting for sample size (Tables 3, 12). The WBNP population is the most diverse population based on allelic richness with rarefaction and its contribution to total diversity, followed by the HLWBRP population. This trend is even greater if just the contribution to diversity for each population is considered. However, when divergence is considered, these populations both have a slightly below average contributions to overall diversity. With rarefaction, the EINPW population is the least diverse (compared to being second least diverse based on allelic richness). EINPW, MB, and YK have negative contributions to the total allelic richness diversity, and all contributions are due solely to within-population diversity.

Table 12. Genetic contribution of each wood bison population to total diversity, measured as mean number of alleles with rarefaction, A^R. C^R_T represents the total contribution of each population to wood bison diversity, C^R_S represents the amount of this contribution due to each population's diversity, and C^R_D represents the amount of this contribution due to each population's divergence.

Herd	A^R	C^R_T	C^R_S	C^R_D
WBNP	5.95	0.07020	0.07590	-0.00597
MB	4.51	-0.00327	-0.01050	0.00703
EINPW	3.85	-0.03970	-0.04980	0.01040
YK	3.89	-0.03130	-0.04720	0.01600
HLWBRP	5.21	0.02960	0.03150	-0.00206

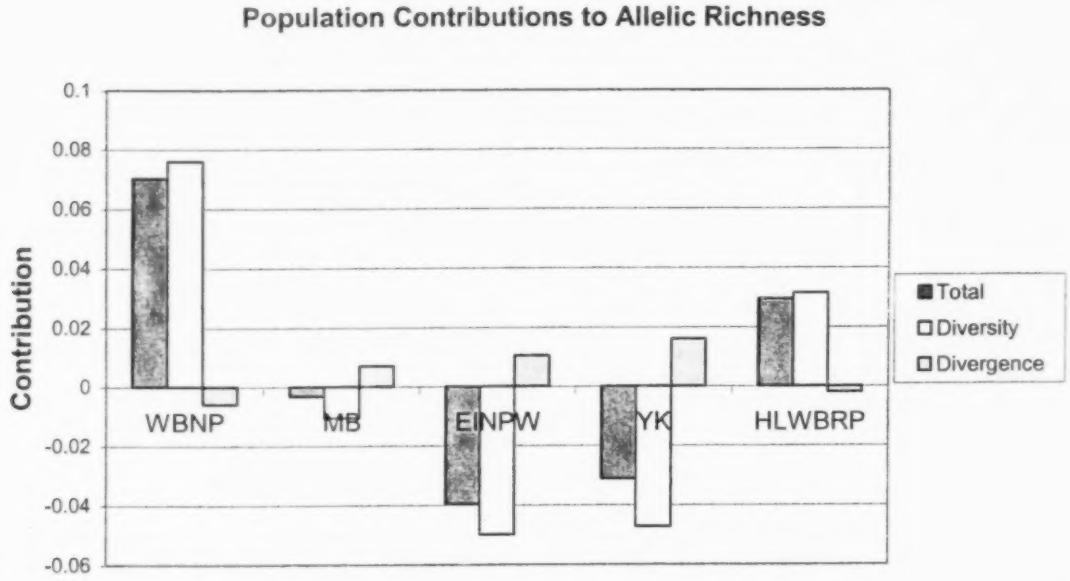

Figure 4. Contributions of each population to total wood bison diversity, measured as allelic richness.

When WBNP is not included in the analysis, only EINPW and, very slightly, MB make positive contributions to the total diversity of wood bison, as measured by expected heterozygosity (Table 13, Figure 5). However, when the contribution from

within-population diversity is separated from that due to divergence, only EINPW and HLWBRP make positive contributions to diversity.

Table 13. Genetic contribution of each wood bison population to the total diversity, measured as unbiased expected heterozygosity when WBNP is excluded from the analysis. Abbreviations are defined in Table 11.

Herd	C_T	C_S	C_D
MB	0.000199	-0.029300	0.029300
EINPW	0.013300	0.019000	-0.005640
YK	-0.004040	-0.002610	-0.001380
HLWBRP	-0.009430	0.012900	-0.022400

Unlike the trend observed for expected heterozygosity, HLWBRP is the only population that makes a positive contribution to diversity based on allelic richness (Table 14, Figure 6). When population divergence is excluded from the calculation, MB also makes a slightly above average contribution to overall wood bison diversity.

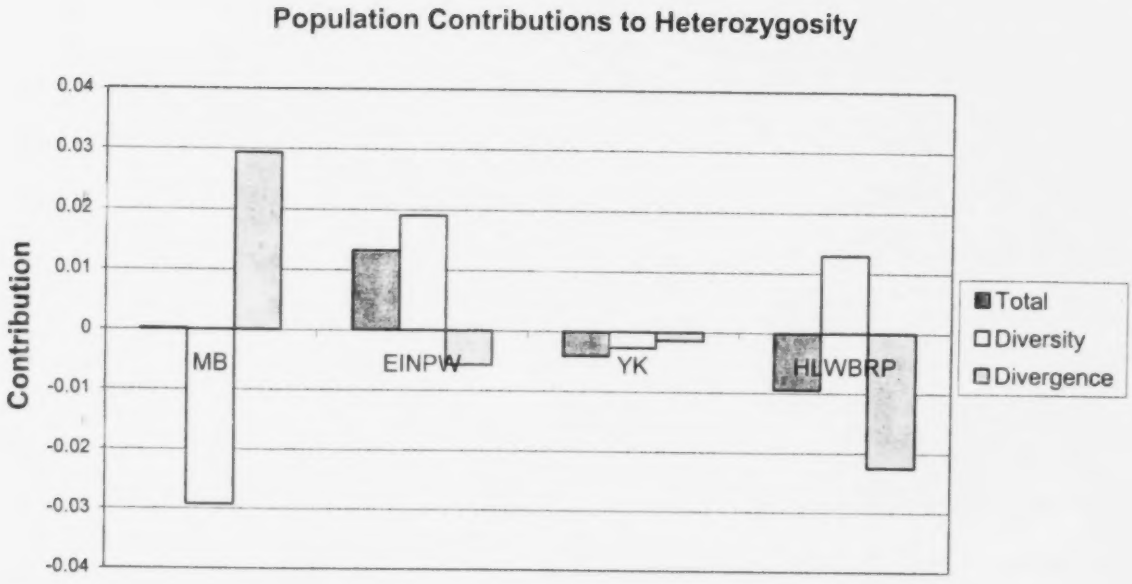

Figure 5. Contributions of each population to total wood bison diversity, measured as unbiased expected heterozygosity, when WBNP is excluded from the analysis.

Table 14. Genetic contribution of each population to overall diversity, measured as mean number of alleles with rarefaction when WBNP is excluded from the analysis. Abbreviations are defined in Table 12.

Herd	C^R_T	C^R_S	C^R_D
MB	-0.003640	0.012900	-0.016600
EINPW	-0.097900	-0.046300	-0.051700
YK	-0.073300	-0.042000	-0.030900
HLWBRP	0.082500	0.075800	0.006570

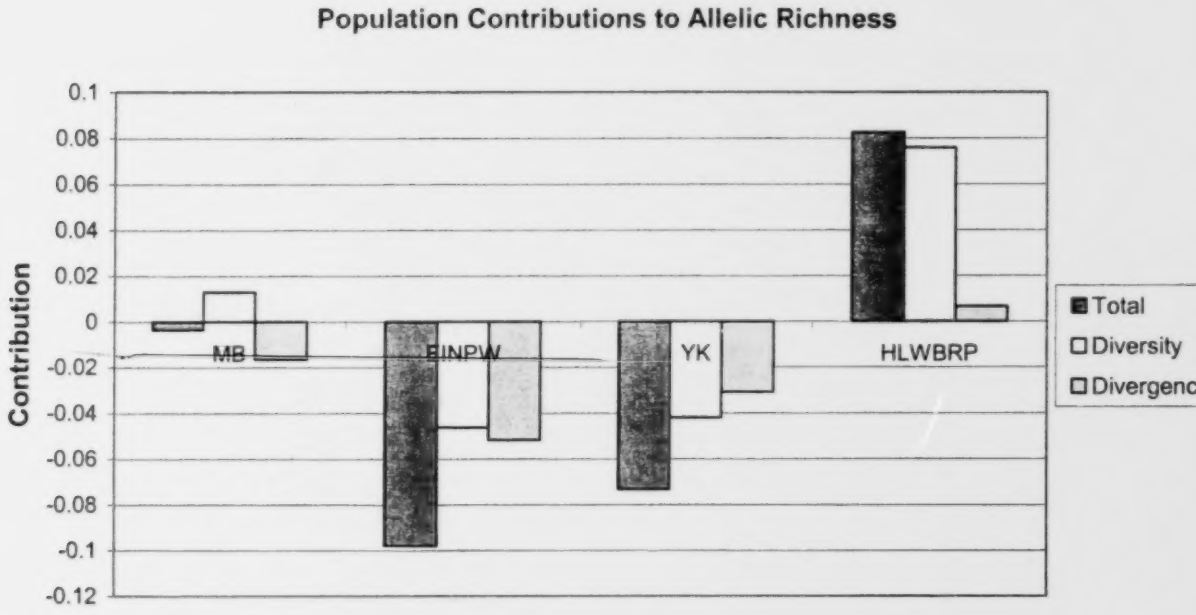

Figure 6. Contributions of each population to total wood bison diversity, measured as allelic richness, when WBNP is excluded from the analysis.

3.2 Future genetic diversity

3.2.1 PVA Scenario 1: Effects of present conditions

When present demographic distributions of each herd were used in the PVA model, along with current harvesting regimens and carrying capacities, WBNP and MB maintain the highest proportion of their existing diversity (Table 15, Figure 7). After 200 years, heterozygosity in WBNP is 99% of its original value and, after 500 years, heterozygosity declined to only 98%. Based on existing diversity, this decline would result in a heterozygosity of 54.4% and 53.8% after 200 and 500 years. Heterozygosity in the MB herd declined to 89% of its original value after 200 years (to 39.4%), and to 88% after 500 years (to 38.8%). EINPW and YK maintain similar proportions of their existing diversity (87% and 85% after 200 years, and 79% and 77% after 500 years;

Figure 7), resulting in heterozygosities of 45.6% and 41.1% for EINPW, and 40.8% and 37.0% for YK. HLWBRP and NQ maintain the smallest proportions of their diversity (75% and 52% after 200 years, and 53% and 35% after 500 years; Figure 7), resulting in 41.0% and 28.0% heterozygosity for HLWBRP. As the current heterozygosity of NH and NQ are unknown, estimates of future heterozygosities cannot be made for these populations. Overall, when considered as a panmictic metapopulation, wood bison lose diversity at a rate similar to that of WBNP (Figure 7).

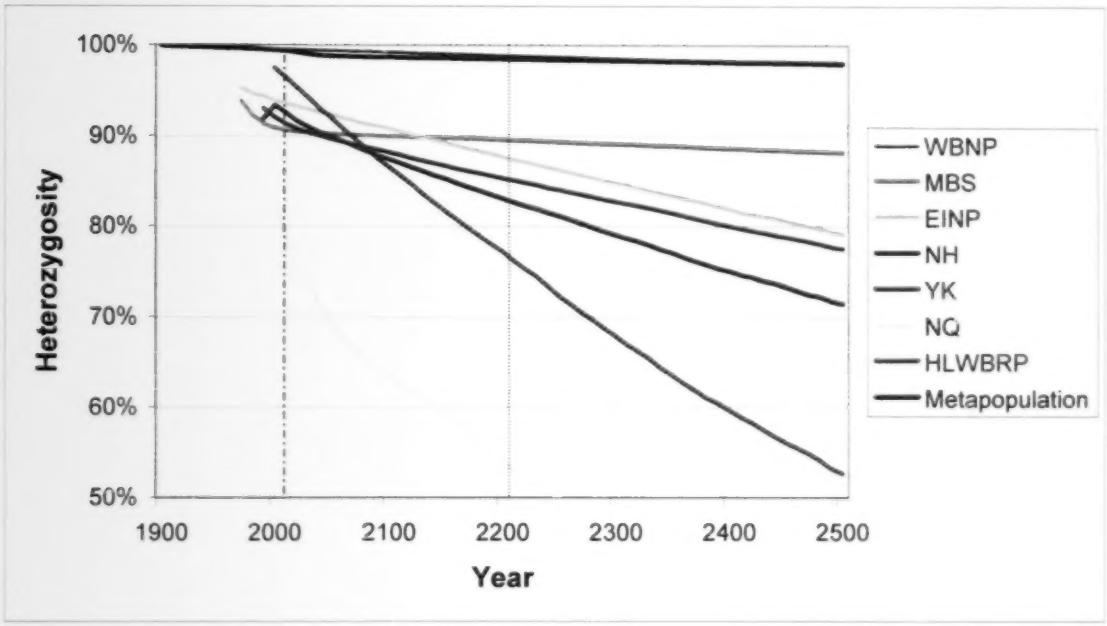

Figure 7. The change in heterozygosity in individual wood bison populations and the entire metapopulation. The dashed line represents the estimated proportion of heterozygosity in 2004. The solid line represents the estimated proportion of heterozygosity after 200 years.

Table 15. Herd size, carrying capacity, and projected heterozygosity of wood bison populations.

Herd	Current Size	Carrying Capacity	Existing He	Projected Percent of Existing He		Projected He	
				200 years	500 years	200 years	500 years
WBNP	4495	4500	55%	99%	98%	54.4%	53.8%
MB	2000	2000	44%	89%	88%	39.4%	38.8%
EINPW	320	450	52%	87%	79%	45.6%	41.1%
NH	200	320 [a]	n/a	83%	71%	n/a	n/a
YK	530	530	48%	85%	77%	40.8%	37.0%
NQ	62	120 [a]	n/a	52%	35%	n/a	n/a
HLWBRP	120	125	53%	75%	53%	41.0%	28.0%
Metapopulation	7727	8040	51% [b]	99%	98%	51.0%	50.0%

[a] Estimate based on current size and expectation that NH and NQ will merge to form a herd of approximately 400.

[b] Calculated as mean heterozygosity for all populations where this value is known, weighted by total population sizes.

3.2.2 PVA Scenario 2: Effects of founding events

When individual herds were modeled independently, assuming unique alleles at the time of establishment, the loss of genetic diversity over time occurred at a slower rate than when herds were founded from WBNP or EINPW (Figure 8). When founding alleles were unique, remaining heterozygosity ranged from 70% (NQ) to 92% (MB and YK) after 200 years, and 47% (NQ) and 91% (MB) after 500 years. Remaining heterozygosity in HLWBRP would be 76% and 55% after 200 and 500 years.

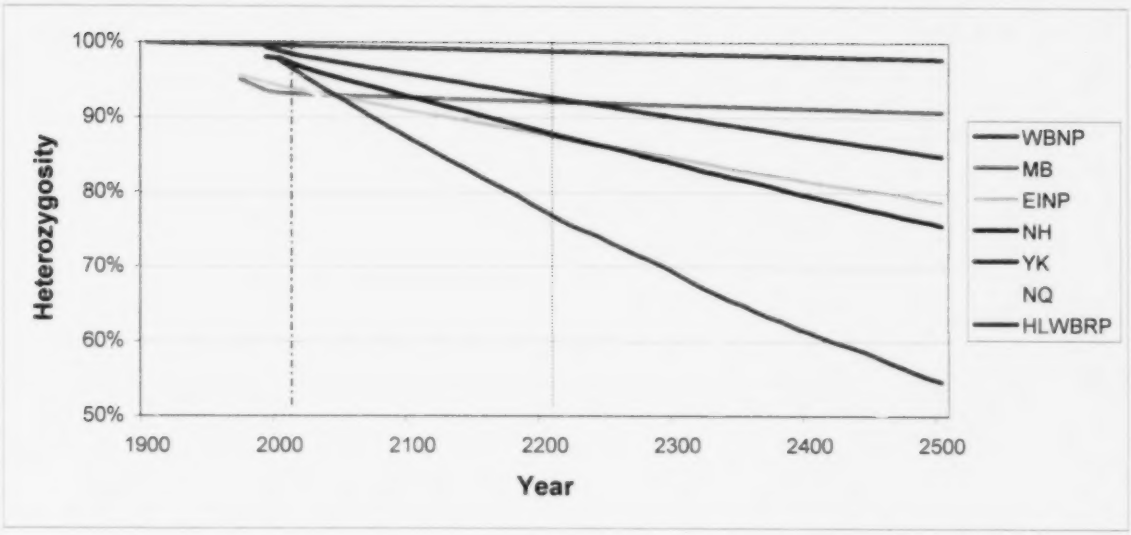

Figure 8. The change in heterozygosity in individual wood bison herds if no founding events had occurred and all alleles in the founding individuals are unique. The dashed line represents the estimated proportion of heterozygosity in 2004. The solid line represents the estimated proportion of heterozygosity after 200 years.

3.2.3 PVA Scenario 3: Effects of multiple herds

Long-term retention of genetic diversity within the wood bison metapopulation is somewhat related to the number of herds within the metapopulation (Figure 9). Over 500 years, the greatest level of heterozygosity is maintained (98%) when either seven or six (all but HLWBRP) herds are established. If only WBNP had been established, or if MB and EINPW were established as well, the loss of genetic diversity would also occur slowly, resulting in retention of slightly less than 98% of each herds' original heterozygosity levels. If WBNP is removed, the metapopulation loses genetic diversity more rapidly, retaining 96% of its original levels after 500 years.

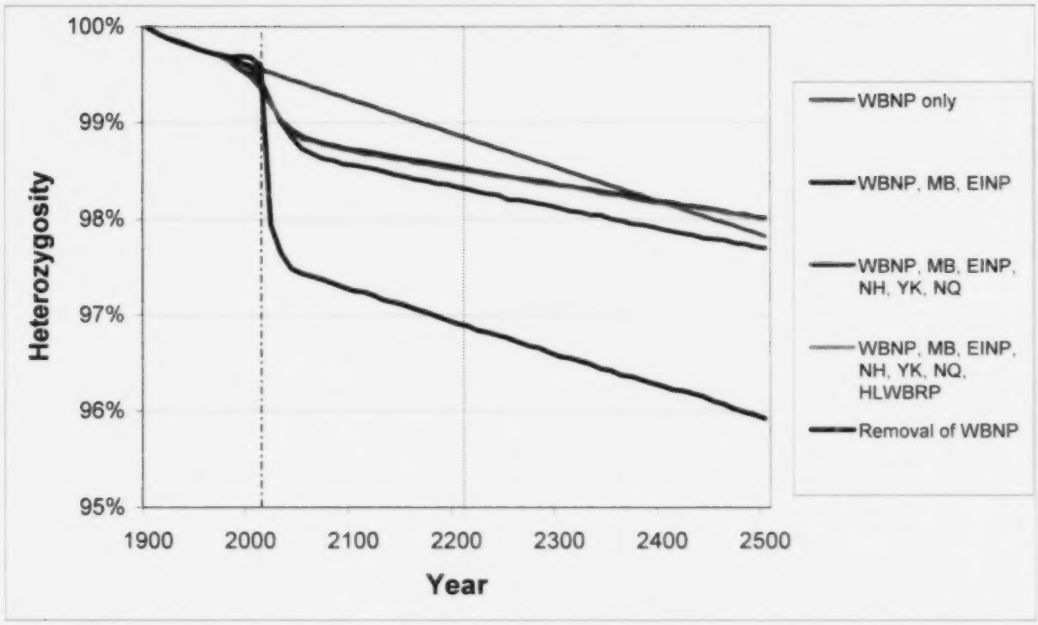

Figure 9. The change in metapopulation heterozygosity as herds are added or removed. The dashed line represents the estimated proportion of heterozygosity in 2004. The solid line represents the estimated proportion of heterozygosity after 200 years.

3.2.4 PVA Scenario 4: Effects of gene flow, regular culling, and additional salvage efforts

Movement of bison among herds will reduce the rate at which genetic diversity is lost from the metapopulation (Figure 10). The number of calves translocated each year also impacts the loss of genetic diversity; it occurs more slowly when 20 calves are moved annually from each herd, compared to 10 calves annually (Figure 11). The slowest rate of diversity loss occurs when gene flow occurs among all herds (99% heterozygosity is maintained after 500 years; Figure 10). Annual translocations of bison from only MB and HLWBRP retain similar levels of genetic diversity (98% heterozygosity after 500 years) to when animals are moved among all herds (99%

heterozygosity after 500 years). When only HLWBRP bison are translocated, high levels (99%) of heterozygosity are maintained for approximately 200 years, after which diversity levels begin to decline (97% heterozygosity is retained after 500 years). Movements of animals from only the MB herd cause the genetic diversity of the metapopulation to decline to 97% its original level after 500 years.

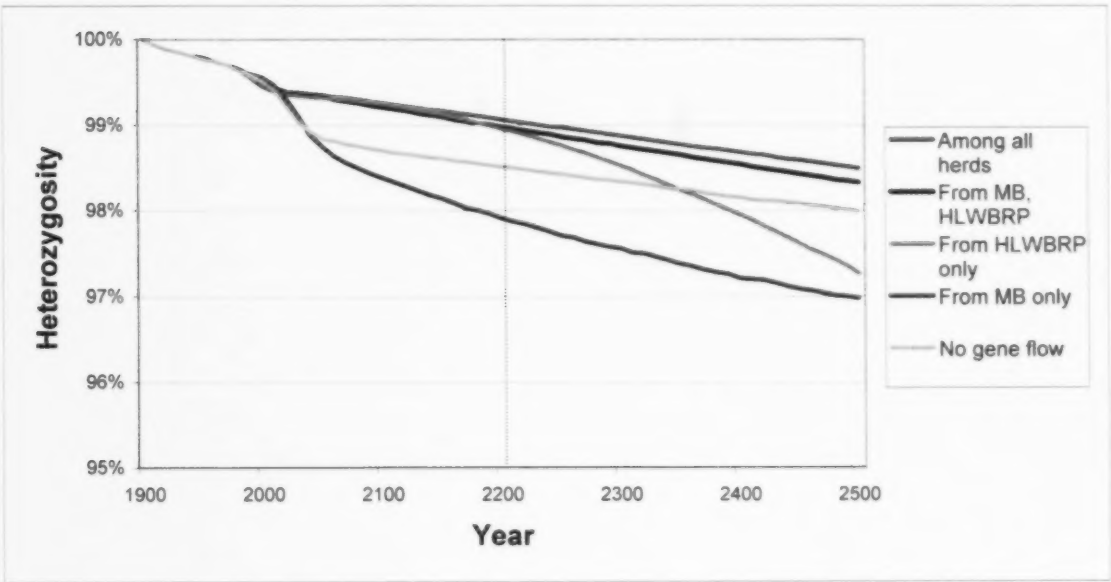

Figure 10. The change in metapopulation heterozygosity as annual translocations occur from MB and/or HLWBRP. Each year, 20 bison calves are moved from all herds (except WBNP), from MB and HLWBRP only, from HLWBRP only, and from MB only. Animals are never translocated into WBNP or HLWBRP. The solid line represents the estimated proportion of heterozygosity after 200 years.

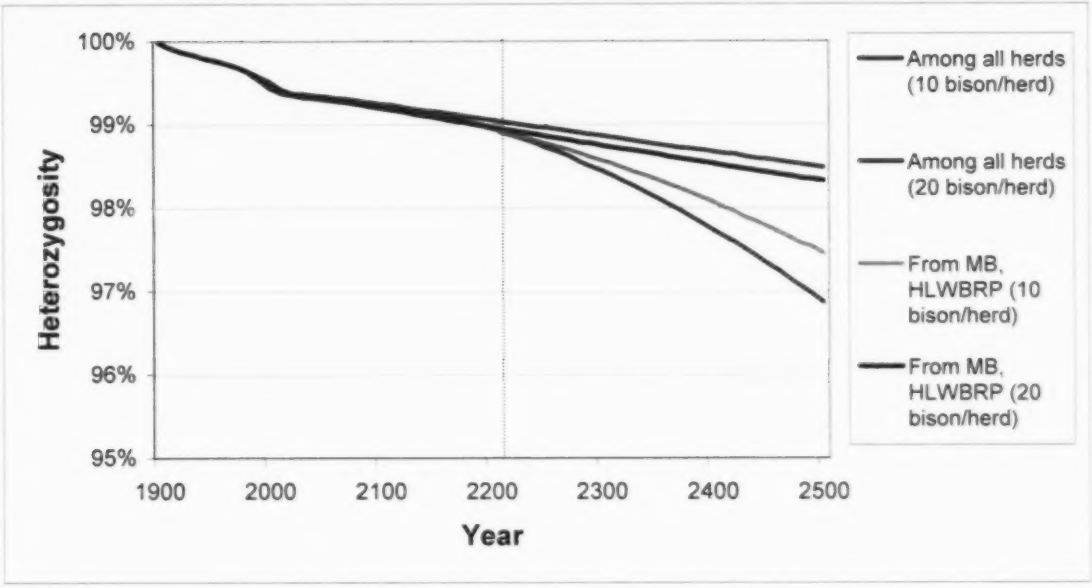

Figure 11. The change in metapopulation heterozygosity as batches of either 10 or 20 bison calves are moved annually. Translocations are modeled to occur from each herd (except WBNP) into all other herds, and from MB and HLWBRP into all herds. Animals are never translocated into WBNP or HLWBRP. The solid line represents the estimated proportion of heterozygosity after 200 years.

When WBNP is removed from the metapopulation, different trends are observed (Figure 12). The greatest amount of genetic diversity is retained when annual translocations occur among all herds (97% heterozygosity after 500 years), followed by when translocations occur from only HLWBRP (96% heterozygosity after 500 years). Movement of animals from only MB or from both MB and HLWBRP cannot retain diversity above the levels predicted if no gene flow were to occur.

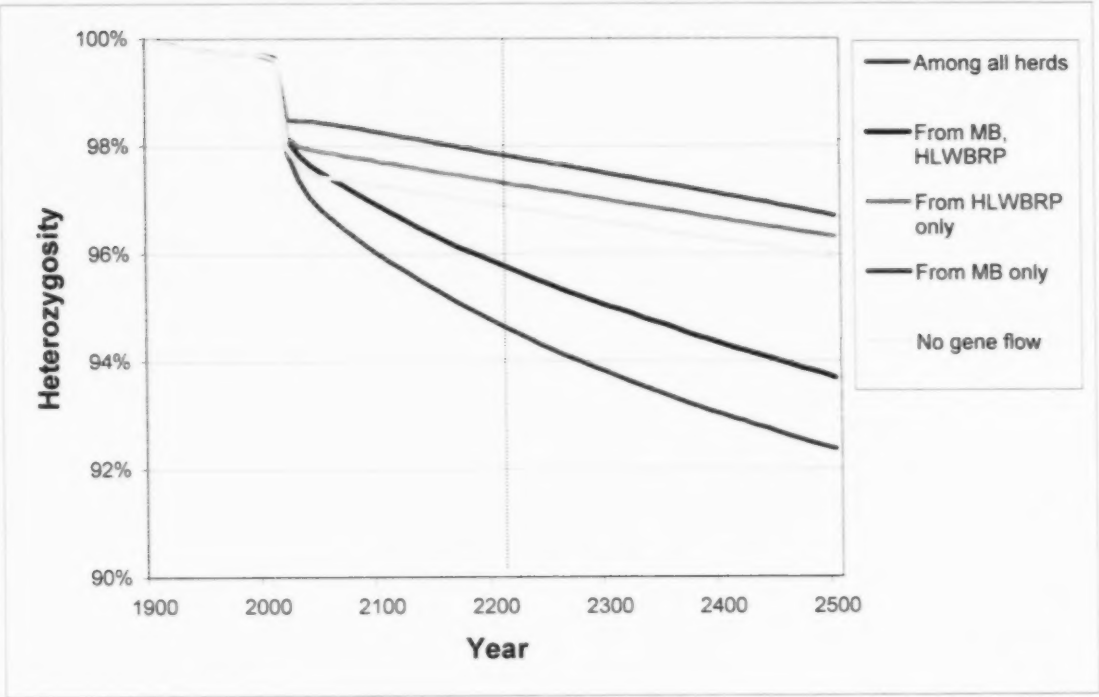

Figure 12. The change in metapopulation heterozygosity as annual translocations occur if WBNP were removed from the metapopulation without additional genetic salvage. This graph represents the heterozygosity in the metapopulation, independent of WBNP. After WBNP is depopulated, 20 bison calves are moved annually from all herds, from MB and HLWBRP only, from HLWBRP only, and from MB only. Animals are never translocated into WBNP or HLWBRP. The solid line represents the estimated proportion of heterozygosity after 200 years.

The genetic effects of moving animals only among the NH, YK, and NQ herds are negligible when WBNP is not removed from the metapopulation (Figure 13). Loss of genetic diversity is projected to occur at a rate comparable to when no gene flow is expected to occur, resulting in 98% heterozygosity after 500 years for both scenarios. Similar results are observed when bison calves are translocated from all herds into only NH, YK, and NQ, and when only bison from EINPW, MB, and HLWBRP are moved into NH, YK, and NQ (98% heterozygosity after 500 years) (Figure 13).

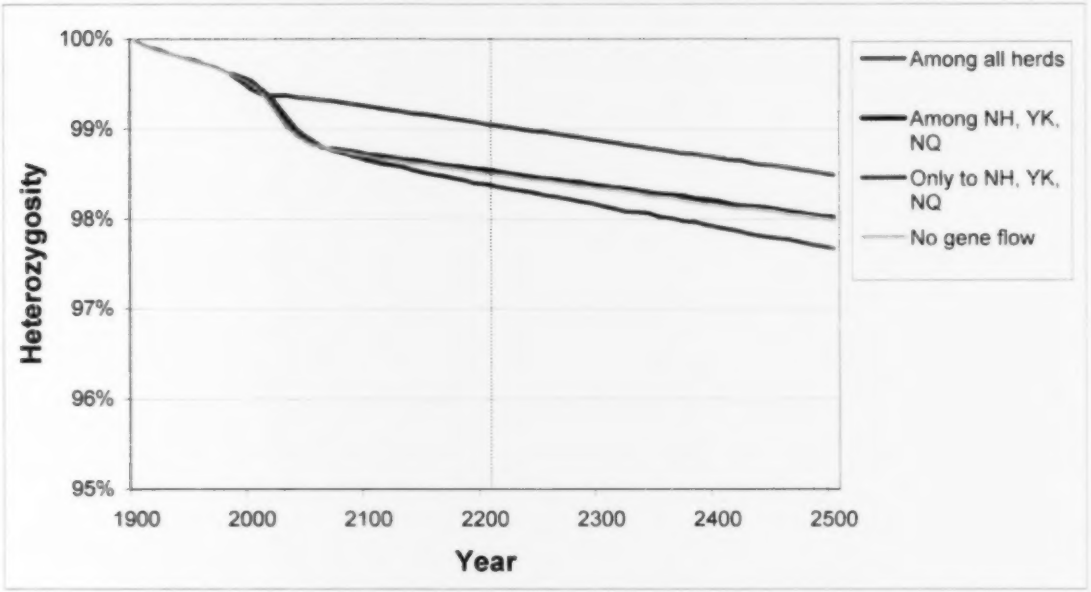

Figure 13. The change in metapopulation heterozygosity as annual translocations involving NH, YK, and NQ animals occur. Each year, 20 bison calves are moved among NH, YK, and NQ, and from all herds (except WBNP) into NH, YK, and NQ. Animals are never translocated into WBNP or HLWBRP. The solid line represents the estimated proportion of heterozygosity after 200 years.

When WBNP is removed, the metapopulation diversity is affected in a similar manner by annual translocations as when WBNP is present. Gene flow among all herds retains the highest proportion of genetic diversity (97% heterozygosity after 500 years; Figure 14). If bison from all herds are moved annually into only NH, YK, and NQ, genetic diversity declines at a faster rate (94% heterozygosity retained after 500 years) than if only bison from NH, YK, and NQ are involved in the annual movements (96% heterozygosity retained after 500 years).

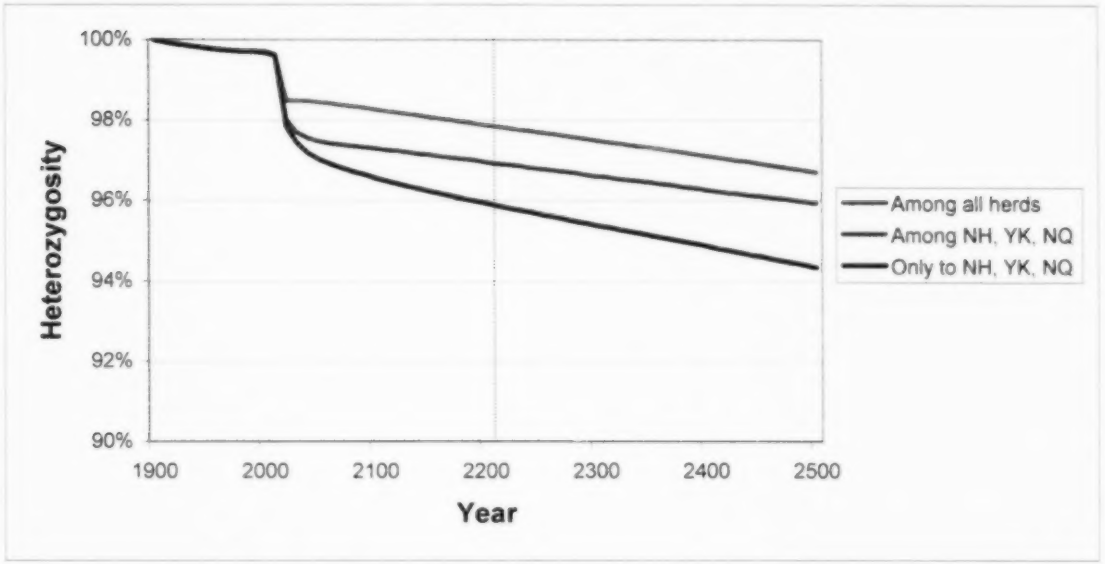

Figure 14. The change in metapopulation heterozygosity as annual translocations occur if WBNP is removed from the metapopulation without additional genetic salvage. This graph represents the heterozygosity in the metapopulation independent of WBNP. After WBNP is depopulated, 20 bison calves are moved annually among all herds, among NH, YK, and NQ, and from all herds (except WBNP) into NH, YK, and NQ. Animals are never translocated into WBNP or HLWBRP. The dotted line represents the estimated proportion of heterozygosity after 200 years.

Additional salvage attempts do not significantly contribute to the maintenance of genetic diversity of the metapopulation (Figure 15). When one and three new wood bison herds are established, the heterozygosity after 200 years and 500 years is approximately 99% and 98%, respectively. Genetic diversity is not significantly different between the two salvage scenarios. The same proportion of heterozygosity (98%) is retained after 500 years when additional salvage efforts are made as when the MB population is expanded to a carrying capacity of 2500.

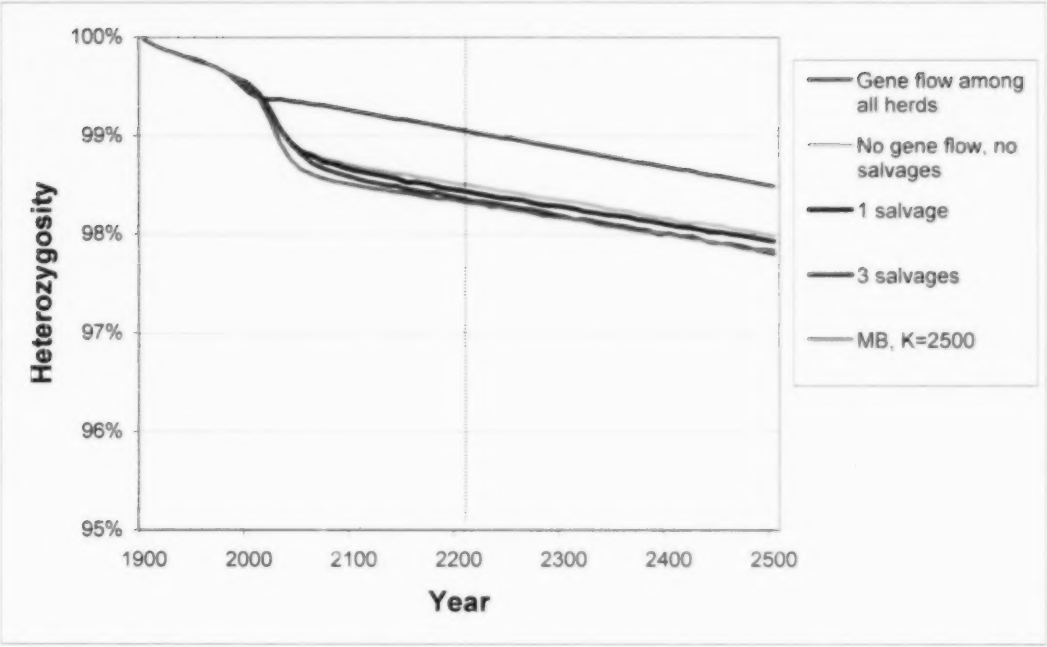

Figure 15. The change in metapopulation heterozygosity as additional salvage efforts are made, as annual translocations occur, and as the carrying capacity of MB is extended to 2500 bison. Salvaged herds are established with the same demographic distributions as the original HLWBRP population. No gene flow occurs when salvage efforts are made or when the carrying capacity of MB is extended. Animals are never translocated into WBNP or HLWBRP. The dotted line represents the estimated proportion of heterozygosity after 200 years.

4.0 Discussion

4.1 Existing genetic diversity in wood bison

A deficiency of heterozygotes was detected for one locus in the YK population, which can be indicative of the presence of null alleles. Null alleles are microsatellite alleles that do not properly amplify during PCR and can thereby skew the observed allele frequencies and subsequent analyses. As Eth121 revealed a significant heterozygote deficiency in the YK population, it is possible that a null allele is present at that locus in YK. However, no evidence for null alleles was observed at this locus in other populations (Wilson and Strobeck 1999). Therefore, Eth121 was not excluded from the analyses.

As shown in Table 3, YK is the least variable of all wood bison populations, based on most diversity measures. This is unsurprising as YK was founded from EINPW animals, which form one of the least variable wood bison populations. The number of cross-assignments between YK and EINPW (Table 5), the relatively small genetic distance between these populations (Table 6), and their grouping on the neighbour-joining tree (Figure 2), show that these two populations are fairly similar genetically. Their similarity is likely a result of the small number of founders for the YK population and the few generations separating the source population from the founding animals.

As shown in Wilson and Strobeck (1999), the WBNP and HLWBRP populations are the two most genetically similar populations, illustrated by the large number of cross-assignments between these populations (Table 5) and their proximate positioning on the tree (Figure 2). This is a more extreme example of the scenario observed

between YK and EINPW, as the HLWBRP population was established from a larger number of founders, and there has been little time for genetic drift to act on this population. Consequently, no population is more similar to WBNP than HLWBRP. In total, less than 2% of wood bison misassigned to a plains bison population. All of these were individuals from WBNP.

For all but two loci, RT24 and BM143, the observed numbers of alleles and expected heterozygosities in YK fell within the 95% C.I. simulated by GENELOSS. The heterozygosity and number of alleles at locus RT24 were below the 95% C.I., whereas diversity at BM143 was above the 95% C.I. Neither RT24 nor BM143 were loci for which an extended data set was available, and therefore initial estimates of diversity by GENELOSS were based on a smaller sample size. Consequently, the low diversity of RT24 can be explained by a sampling bias. Furthermore, the observed diversity in the YK population could be biased as only a small proportion of this population was collected for DNA sampling.

The large number of observed alleles and expected heterozygosities at BM143 could be explained by incomplete sampling in the EINPW population. More alleles were seen at locus BM143 in the YK population than in EINPW, the founding population. Three possible scenarios could explain this result; the new allele arose by mutation early in the YK population's history and rose to an appreciable frequency through genetic drift, it was present in the EINPW population but has since been lost, or it is still present in the EINPW population but was not sampled. Of these the last situation is the most likely, given the low rate of mutation, the probability of quickly losing an allele from

EINPW given its sample size, and the relatively small proportion of the EINPW population that were sampled at this locus.

Another factor potentially affecting the results of this simulation is that samples collected in 1998 in EINPW are being used to estimate those from 1986. It is possible that genetic drift over this time period would have altered the allele frequencies in EINPW. However, given the large size of this population and the small number of generations since that time, any changes would likely be minimal. Finally, it should be noted that while most of the observed genetic diversities fall within the 95% C.I., the standard deviations of the simulated values tend to be large (Tables 7, 8).

All simulated measures of diversity for the NQ population were less than those simulated for the YK population, owing to the consistently smaller number of reproductive pairs for NQ. The simulated number of alleles for the NQ population was smaller than that observed in any other bison population (Table 9). Simulated heterozygosity values for NQ were smaller than those seen in the YK population, except for the case of a 2-generation bottleneck of 8 reproductive pairs (Table 10). Thus, simulations suggest that the NQ population is one of the least, if not the least, genetically diverse wood bison population examined to date.

WBNP contains over 97% of the alleles observed in wood bison, and seven of the eight private alleles (Table 3). A sizeable proportion of wood bison genetic diversity is represented only in this herd. Both allelic richness and private alleles are dependant on sample size, however, and the largest samples were obtained from this population. Therefore, some of these alleles may exist in other populations, but remain unsampled. As expected from looking at other measures of diversity (e.g., heterozygosity and

probability of identity), the YK population contains the lowest proportion of the alleles found in wood bison. When WBNP is not considered in the analysis, HLWBRP became the population with the highest proportion of wood bison alleles (92%), and the largest number of private alleles (Table 4). The HLWBRP contained the largest amount of diversity found in WBNP, and was therefore a valuable resource of wood bison genetic material.

The genetic importance of the WBNP population to wood bison diversity is evident with both the expected heterozygosity and, especially, the allelic richness with rarefaction measures (Figures 3, 4; Tables 11, 12). Both of these measures are relatively unaffected by sample size. In both instances, the importance of WBNP is even greater when the contribution due to divergence is removed, leaving only the diversity contribution. This is a result of the relatively small genetic distances between WBNP and the other wood bison populations, particularly the HLWBRP (Table 6).

It may be essential to consider the contribution of divergence to genetic importance when populations share a small number of alleles, or if population divergence is a result of differential selection regimes. However, private alleles are generally uncommon in bison populations and founding events, rather than selection, largely control population relationships. Consequently, the diversity contribution is the primary factor that should be considered for genetic importance.

HLWBRP was the only other population to make a positive contribution to the diversity portion of genetic importance with both measures (Figures 3, 4; Tables 11, 12). However, the overall contribution of HLWBRP to heterozygosity was negative, due to the large negative contribution to the divergence portion of genetic importance. This

was likely a result of the close relationship between HLWBRP and WBNP, due to the recent founding event of HLWBRP from WBNP that included a large number of individuals. Also, genetic distances between HLWBRP and other populations tend to be smaller than those distances not involving HLWBRP or WBNP (Table 6).

To determine the importance of wood bison populations if WBNP is removed from the gene pool, genetic importance was recalculated without this population. Both EINPW and, slightly, MB had positive total genetic importance values when heterozygosity was considered (Figures 5, 6; Tables 13, 14). However, EINPW and HLWBRP were the populations that contributed positively to the diversity portion of heterozygosity. HLWBRP was the only population that positively contributed to the genetic importance of allelic richness values, and was joined by MB when only diversity was considered. Allelic richness is commonly described as the most relevant measure of genetic diversity (Schoen and Brown 1993, Bataillon *et al.* 1996, Petit *et al.* 1998). Consequently, if WBNP were removed from the wood bison metapopulation without additional genetic salvage, the HLWBRP would have become the most important source of genetic diversity.

4.2 Projected genetic diversity based on current management scenarios

Based on present demographic distributions, current harvesting regimens, and existing carrying capacities, the projected genetic diversity of each herd declined at a rate relative to the herd's population size (Figure 7). WBNP and MB are the largest herds (N = 4495 and N = 2000, respectively (M. Bradley and J. Nishi, pers. com. 2004)) and maintain the highest proportion of their existing diversity over 500 years (98% and 88% heterozygosity, respectively). EINPW (N = 320) and YK (N = 530) have similar

herd sizes and maintain similar proportions of their existing diversity after 500 years (79% and 77% heterozygosity). The smallest herds, NH (N = 200), HLWBRP (N = 120), and NQ (N = 62), maintain the smallest proportions of their diversity (71%, 53%, and 35% heterozygosity). Herds that can retain larger sizes are better able to maintain existing levels of genetic diversity, as the influence of genetic drift is inversely proportional to population size. Furthermore, density would not be as considerable a limiting factor of mean generation time for individuals belonging to populations on a large range.

Although population size has a significant influence on the ability of a herd to retain genetic diversity, loss of genetic diversity is also impacted by several other demographic factors. The number of founding events or bottlenecks experienced by a herd affects the initial level of diversity within that population (Figure 8). The WBNP population, which experienced only a single recent bottleneck, contains the highest levels of genetic diversity (Tables 3, 4). The EINPW, MB, and HLWBRP populations were founded from WBNP animals and contained relatively large levels of initial diversity. As HLWBRP was established from the largest group of WBNP founders, its initial diversity was high. In comparison, the NH, YK, and NQ populations, which were established from EINPW animals, experienced two founding events and could not contain more diversity than that present in EINPW at the time of their inception.

Using most measures, WBNP, EINPW, and HLWBRP had the highest levels of genetic diversity (Table 3). After 500 years, WBNP and EINPW are still expected to have the highest levels of diversity (Figure 7; Table 15). HLWBRP, on the other hand, was projected to rapidly lose diversity due to its small population size and carrying

capacity (and see Wilson *et al.*, 2005). Genetic management was necessary for the small HLWBRP herd to maintain high diversity in the long term. Consequently, given the operational and economic constraints for carrying capacity at the HLWBRP, we developed a captive breeding and genetic management plan to reduce the rate of loss in genetic diversity at the HLWBRP (Wilson *et al.* in prep).

Despite its larger size and consequent slower rate of diversity loss, MB will be less variable than EINPW after 500 years due to the current higher level of diversity at EINPW (Table 15). Both the MB and EINPW herds were founded from WBNP bison in the 1960s, but the number of founders for the EINPW population was slightly higher (Table 1). The stochastic processes of genetic drift since that time could also have had varying effects on the diversity within these populations.

Both NQ and NH are expected to lose diversity at a rate relative to their herd size. Simulations suggest NQ is among the least variable wood bison populations. Current levels of diversity for NH are unknown.

4.3 Contribution of herds to the future metapopulation diversity

Although the rates at which individual herds lose genetic diversity vary, the metapopulation maintains diversity at approximately the same rate as the WBNP herd (Figures 7, 9). As well as being the largest herd, comprising roughly 60% of the wood bison metapopulation, WBNP is also the founding population for all other wood bison herds and contains a significant proportion of the diversity within the metapopulation (Tables 11, 12). Depopulation of WBNP without salvage would significantly reduce the overall diversity of Canadian wood bison (Figure 9). However, depopulation with adequate genetic salvage would prevent or minimize this loss of overall diversity.

There is a slight inverse relationship between the number of herds in the metapopulation and the rate at which diversity is lost. As the contribution of WBNP to the metapopulation diversity is so large, the rate of diversity loss does not significantly differ between scenarios when only WBNP, or only WBNP, EINPW, and MB, or all but HLWBRP, or all seven herds are established. However, although values are similar, the rate at which diversity would be lost from a WBNP-only scenario is greater than that of a multiple herd scenario (Figure 9). It would therefore follow that the establishment of new herds should assist with the long-term conservation of genetic diversity, especially if WBNP is depopulated. Also, additional herds act as genetic banks, which could provide genetic material if any existing population is lost from the metapopulation.

4.4 Metapopulation management and projected genetic diversity

Periodic movements of animals among herds will significantly contribute to the overall diversity of the metapopulation. Our results suggest that establishing gene flow among all herds will be the best way to preserve the long-term genetic diversity of wood bison in Canada (Figures 10 -14). However, with respect to the contribution of unique genetic diversity, gene flow from HLWBRP, or MB and HLWBRP, would be most important (Figures 10, 12). This is because, aside from WBNP, all other herds are founded from EINPW animals and should be genetically similar to this population, although with lower levels of diversity. As such, they likely share a large amount of genetic diversity with one another, and movement of animals between these herds would not be the most efficient method of adding new genetic material to these populations. Translocations of animals from HLWBRP, or MB and HLWBRP, would provide new genetic material to herds founded by EINPW. Nonetheless, as populations

drift and become more dissimilar over time, moving animals from EINPW to other populations may increase metapopulation diversity. The movement of additional EINPW animals can also overcome the effects of founding events in cases where the number of founders was small and did not contain a representative amount of diversity.

Although movements of animals from both MB and HLWBRP could significantly contribute to long-term maintenance of diversity, translocation of animals from HLWBRP would have had the greatest effect (Figures 10, 12). Movements of animals solely from the MB herd will be insufficient for maximum retention of genetic diversity. This is likely due to the small founding size of the herd (N = 16). In comparison, due to its relatively large founding size (N = 57) and recent founding event, HLWBRP possessed the greatest amount of genetic diversity and would have therefore contributed more variation to the metapopulation (see Wilson *et al.*, 2005). From a theoretical perspective, annual gene flow from HLWBRP over a 200-year period would have contributed the most to overall metapopulation diversity (Figure 10). However, after 200 years of moving bison out of HLWBRP without bringing additional animals into the small herd, the genetic diversity of HLWBRP would decline drastically, likely as a result of genetic drift in this small population (Figures 10, 12). The overall diversity of the metapopulation will similarly decrease due, in part, to the loss of diversity from HLWBRP, as well as from the dilution of unique genetic material as animals are moved from a small, diverse population into large, less-diverse populations. These results reinforce the importance of maintaining HLWBRP at a sufficient size to preserve genetic diversity levels that are representative of the founding population.

The genetic effects of moving animals only among the NH, YK, and NQ herds are negligible because each of those herds were founded from similar genetic stock and currently have lower diversity than most other herds (Figures 13, 14; Table 15). Consequently, moving animals between these populations conserves a similar amount of genetic diversity as scenarios where no gene flow occurs. Furthermore, if gene flow were to occur from any herd, except WBNP, into only NH, YK, and NQ, genetic diversity will be lost at a faster rate than if no gene flow occurred (Figures 13, 14). This may be a result of the homogenization of genetic diversity in a number of populations as individuals from a less diverse source are moved between populations.

For the optimum preservation of genetic diversity for 500 years, translocations of bison among herds should involve as many animals as possible. For 200 years, the number of bison involved in the translocation does not significantly impact the rate at which diversity is lost (Figure 11). However, beyond 200 years, genetic diversity can be best maintained when 20 bison are moved from each herd annually, rather than only 10 bison from each herd annually. Movements of twice as many animals will incorporate a greater proportion of the existing genetic diversity into each herd. Although translocations occurred annually in our model, biannual movements of twice as many calves would be acceptable for preserving long-term genetic diversity. Moreover, biannual movements of twice as many calves may actually improve the retention of genetic diversity in the metapopulation, because entire cohorts could be removed together. This would not reduce the existing diversity of the source herd and adults could contribute their genetic material to the next generation during the following season. Unfortunately, this scenario cannot be tested using VORTEX. However, the

culling of calves biannually has been shown to be the most efficient method for maintaining diversity at EINPW (Wilson and Zittlau 2004).

Regardless of the degree of gene flow established among herds, maintenance of large sizes will be important. Movement of animals should not occur if the herd size would be significantly reduced. Maintenance of herd size at approximately carrying capacity will minimize loss of diversity over time. However, without the influence of gene flow, an increase in carrying capacities of currently large herds will not significantly affect the metapopulation diversity (Figure 15). No change in the metapopulation diversity is observed when the carrying capacity of MB is increased from 2000 to 2500. In comparison, an expansion of the ranges of the smaller herds (e.g., NQ, NH, and HLWBRP) will likely have a considerable effect on the long-term preservation of diversity, particularly when gene flow is included. As this is not currently a viable option, the scenario has not been modeled.

Simulation results indicate that the establishment of one or three new herds provides no additional advantage to preserving genetic diversity of the overall wood bison metapopulation over the current scenario of no gene flow, so long as the WBNP population remains in existence (Figure 15). This is because WBNP currently has the greatest influence on metapopulation diversity, due to its large size. However, as recovery of wood bison is intrinsically tied to management of diseased populations (see Gates *et al.* 2001), additional salvage efforts will be essential for conserving and providing genetic material that is representative of WBNP, if diseased populations are to be removed from the metapopulation (see Shury *et al.* 2006).

Since each additional salvage attempt increases the ability of the metapopulation to maintain diversity, and the probability that a representative sample of the diversity within WBNP will be sampled, the establishment of new herds from WBNP will contribute significantly to the long-term conservation of diversity in disease-free wood bison. This is especially true if WBNP is to be depopulated. WBNP has the greatest genetic diversity of all wood bison herds. However, because bison in and around WBNP are infected with bovine tuberculosis and brucellosis, additional salvage efforts from these infected herds will require well-defined criteria, protocols, and health monitoring to establish successful eradication of these diseases. It will be important to conduct decision-making within an *a priori*, formalized, transparent risk-assessment process. This would allow managers to understand and balance the risk of disease transmission against the long-term benefits of increasing genetic diversity in bison populations (see APFRAN 2003, Lutze-Wallace *et* all 2006, Nishi *et al.* 2002a, 2002b, and 2004), and to provide an acceptable level of confidence that disease will not be introduced into healthy herds through management action.

Harvesting or culling also plays a significant role in the long-term conservation of genetic diversity. Previously, it was determined that, for EINPW, biannual removal of a group of calves and yearlings that represent 35% of the total herd size minimizes the loss of diversity over time (Wilson and Zittlau 2004). For other herds, optimal harvesting strategies from a genetic management perspective have yet to be determined. However, previous results suggest that regular culling of an equal number of young males and females can considerably slow the rate at which diversity is lost if a population is at carrying capacity. This occurs for several reasons. First, by removing

calf or yearling animals every second year, mature bison will persist in the population longer and have an increased opportunity to contribute to the gene pool before they die. Second, mature individuals that may not have successfully bred are less likely to be removed from the population. Finally, the mean generation time of the population will be increased because older individuals will be permitted to persist in the population longer. Since diversity is lost when individuals die, this can greatly reduce the population's loss of diversity.

As natural populations will undoubtedly change over time, management actions, such as the maintenance of habitat carrying capacities, regular translocations of calves, additional salvage efforts, and the targeting of young animals during biannual harvests, should be applied to test and evaluate the predictions made in this report at various time-points. It is critical to keep in mind that the predictions produced by the models examined in this report are dependant on both the assumptions of the model and the information supplied to the model. If these assumptions are found to be invalid, or the model parameters change dramatically, the predictions made by the model may no longer apply. Regular application and monitoring of recommended management actions will ensure that appropriate goals are still being targeted. Revisions to management priorities can be addressed as additional knowledge is acquired and alternative hypotheses are evaluated.

5.0 Conclusions

WBNP is the most genetically diverse population of wood bison, based on all measures. This population contains more unique diversity than any other population, and almost all wood bison diversity is represented within WBNP. As a result, WBNP is the most genetically important wood bison population, despite having low divergence values compared to other populations. If the diversity within this population were unavailable, HLWBRP would have become the most genetically important population, based on its allelic richness and the proportion of the remaining metapopulation diversity it would contain.

In most scenarios modeled, the wood bison metapopulation is able to maintain a suitable proportion of diversity over 500 years. The mean genetic diversity projected over time varies according to individual herd sizes, the number of herds in the metapopulation, and the degree of gene flow among herds. Population size has the most significant effect on the rate at which genetic diversity is lost. Maintenance of herd sizes at approximately carrying capacity (or a minimum population size of 400-500 or greater – see Wilson and Zittlau 2004) will best contribute to the long-term retention of genetic diversity.

In addition to large sizes, the number of herds among which gene flow occurs will significantly influence genetic diversity over time. The HLWBRP was an important herd due to its large number of founders, and high levels of genetic diversity that were nearly representative of WBNP. Gene flow from HLWBRP to other herds would have considerably reduced the rate at which diversity was lost. Maintenance of HLWBRP at as large a size as possible and management for diversity would have permitted long-

term future translocations from this herd without significantly impacting the HLWBRP diversity. If the HLWBRP was maintained at its carrying capacity and translocated animals were removed at random, genetic diversity would begin to decline more rapidly after 200 years due to the regular removal of bison without additions to the herd.

With the recent depopulation of the HLWBRP – due to the presence of bovine tuberculosis – the importance of additional salvage efforts is increased. Correspondingly, salvage of new herds from WBNP will be required in order to increase genetic diversity to the rest of the metapopulation. If established from appropriate numbers of founders, additional salvaged herds should also have high diversity that is representative of WBNP. Each additional salvage attempt will increase the diversity of the metapopulation.

The harvesting regimen of each herd will be an important consideration for managers. If a herd is at carrying capacity, regular culling or harvest of an equal number of young males and females should considerably reduce the loss of diversity over time. From a genetic conservation perspective, the removal of the youngest possible animals every second year would provide the best approach to maintaining diversity.

Population dynamics shift over time, so the management actions evaluated in this study should be monitored as new information is gathered and efforts are applied. Population simulations are dependant on model assumptions and the available population and species information. A change in the acceptance of any of these values can alter the expectations arising from a simulation. Consequently, new information

should be incorporated into new simulations when available and management strategies should be revised accordingly.

6.0 Recommendations

In this study, we incorporated genetic data with demographic data from seven wood bison herds in Canada. By combining current knowledge with simulated future changes in genetic diversity, we identified potential management strategies and evaluated the impacts of these strategies on genetic diversity over time. Based on the direction and severity of these impacts, several management strategies are recommended.

1. As the wood bison population at WBNP is the most genetically important for metapopulation diversity, further genetic salvage should be performed from WBNP to ensure the short- and long-term conservation of genetic diversity is managed in disease-free populations. If salvage is based on capturing live animals, genetic management (i.e., determination of the number of founders and breeding management) should reflect the technical knowledge gained from the HLWBRP. The goal of genetic salvage should be to sample high levels of genetic diversity that are representative of WBNP, with an appropriate number of founders. With every additional herd established, the diversity of the metapopulation will be increased. A useful strategy for genetic salvage of disease-free herds from the infected populations in and around WBNP would be to establish individual populations with large numbers of founders (i.e., $\geq$ 50). This should be followed by a rapid growth phase through monitored and/or managed breeding to a population size of at least several hundred.
2. The genetic importance of populations should be considered when choosing founding animals for newly established populations. Those with high importance should be given precedence as salvage sources.

3. The HLWBRP was one of the most genetically important populations, and based on the premise that it was disease-free, it was considered the most important healthy source herd for translocations. However, the confirmation of tuberculosis in the herd (June 2005) and the subsequent depopulation of the HLWBRP (March 2006), re-emphasizes the difficulty, importance, and need for additional genetic salvage. Salvage projects such as the HLWBRP require proper breeding and genetic management, because due to their small size, diversity can be lost quickly.
4. Larger wood bison herds (i.e., a census population size of several thousand) lose less genetic diversity over time. Therefore conservation herds should be maintained at their approximate carrying capacity to minimize loss of diversity. Over meaningful time, herd size is the most significant aspect affecting genetic diversity. Therefore, if the carrying capacity of any herd could be increased, loss of genetic diversity will be slowed accordingly. This is especially true for the smaller herds (i.e., less than a few hundred).
5. Gene flow among all healthy herds will significantly reduce the rate at which diversity is lost. Annual movements of 10 male calves and 10 female calves are recommended, although biannual movements of 20 male calves and 20 female calves are likely to have equivalent effects on the retention of genetic diversity.
6. If herd reductions are required, biannual removals of an equal number of young males and females will significantly slow the loss of genetic diversity over time. Herds should be at carrying capacity before regular removals are initiated.

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